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Systematics of the *melanocephala* Group of the Colubrid Snake Genus *Tantilla*

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Systematics of the *melanocephala* Group of the Colubrid Snake Genus *Tantilla*

Larry David Wilson and Cesar E. Mena

Abstract. The *Tantilla melanocephala* group is herein recognized as comprising 6 species. These are *Tantilla andinista*, sp. nov., *T. capistrata*, *T. equatoriana*, sp. nov., *T. insulamontana*, sp. nov., *T. lempira*, sp. nov., and *T. melanocephala*. The nominal species *Tantilla armillata*, *T. fraseri*, *T. longifrontalis*, *T. mexicana*, and *T. ruficeps* are synonymized with *T. melanocephala*.

Tantilla melanocephala is composed of 6 pattern groupings (A-F), 2 of which (C and D) are sympatric. The status of the 11 names associated with the *T. melanocephala* population system is discussed.

A key for the identification of the 6 species of the *T. melanocephala* group and the 6 pattern groupings of *T. melanocephala* is provided.

The distribution of the *Tantilla melanocephala* group encompasses most of Central America and much of South America. The nominate species occupies most of the range of the group and the other 5 species are scattered along the periphery of the northern and western portions of the range. A wide range of physiographic types is inhabited by members of the group ranging from coastal lowlands to the high mountains of the Andes. The altitudinal range is from sea level to 3080 m. A broad range of phytogeographic types is inhabited as well, ranging from pineland and tropical lowland rain forest to montane rain forest and from coastal deserts to semiarid intermontane basins.

Study of the relationships and evolution of the members of the *Tantilla melanocephala* group indicates that climatic fluctuations in the Pleistocene and Holocene epochs have acted alternately to fragment and rejoin segments of the group so as to produce a picture of varying degrees of relationships of the included taxa one to another. Data derived from study of evolutionary trends suggest that the pattern E group of *T. melanocephala*, now occurring in the upper reaches of the Amazon Basin, is closest to the evolutionary stock of the group. *Tantilla equatoriana* and *T. insulamontana* appear to be early offshoots of the basal stock isolated by the uplift of the Andes in the upper Pliocene and lower Pleistocene. *Tantilla andinista* may have been isolated in an Andean intermontane basin at around the same time. The pattern A group of *T. melanocephala—T. lempira* stock then may have moved into Central America during an arid interglacial phase. The pattern B and F groups appear to have branched off next, becoming isolated from other members of the group and from one another in different forest refuges in northern Colombia. The pattern C-D stock next moved throughout the Amazon Basin during a wet glacial phase and gave rise to *T. capistrata*, which became isolated in the coastal desert and the region of the Porculla Pass in Perú.

Introduction

The *melanocephala* group of the colubrid snake genus *Tantilla* has been particularly void of any illuminative scrutiny for most of its history. This history has been characterized largely by the addition of new species to the group within the period from 1758 to 1896. The fundamental questions concerning the taxonomy of this group of *Tantilla* have remained unanswered during the present century and what work has been done on the group has dealt with only small segments of the overall problem (e.g., Smith, 1942; Peters, 1960).

This study is concerned with the entire scope of the *melanocephala* group (as defined herein-see below) and is one of a series of papers dealing with the Neotropical species of *Tantilla*. This study began with a consideration of the status of *Tantilla armillata* Cope in connection with the work by John R. Meyer and the senior author on the Honduran snake fauna. The study quickly expanded to include all species of *Tantilla* with a dark middorsal stripe. At an early stage of this project we segregated a group of 4 closely related species of Mexican *Tantilla* with a dark middorsal stripe from others in Central and South America and considered the former *(calamarina)* group in the Meyer and Wilson work mentioned above. The present paper thus is restricted to the consideration of those species we consider to comprise the *melanocephala* group.

Color Pattern Terminology

Due to the relatively complex nature of the color pattern of the head and neck of members of the *Tantilla melanocephala* group, it is necessary to provide the following definitions:

1. Dark head cap—the portion of the head pattern occupying most of the dorsal portion of the head;
2. Pale nuchal band—the pale band, which may be divided medially or medially and laterally, located on the posterior portion of the parietals and a variable number of dorsal scales posterior to the parietals;
3. Dark nape band—the dark band, of variable length (absent in one species), following the pale nuchal band;

4. Pale neck band—the narrow pale band following (if present) the dark nape band.

Delineation of the *melanocephala* Group

The term "*melanocephala* group" has been used only 3 times in the literature, so far as we are aware. The term was first used by Smith (1942), who included *T. armillata*, *T. deppei*, and *T. mexicana*. Mertens (1952) used the phrase and indicated that *T. armillata* is a member. Finally, Stuart (1963) included *T. mexicana* and *T. armillata*. In all cases, obviously, the implication is that *T. melanocephala* is also a member.

Other scattered pieces of information from the literature indicate tacitly that 6 nominal species comprise the *melanocephala* group: *Tantilla armillata* Cope, 1876*a* (type locality: "middle Costa Rica"); *T. fraseri* Günther, 1895 (Quito, Ecuador and "W. Ecuador"); *T. longifrontalis* (Boulenger), 1896*b* (Cali, Colombia); *T. melanocephala* (Linnaeus), 1758 ("America"); *T. mexicana* (Günther), 1862 ("Mexico"); *T. ruficeps* (Cope), 1894 ("Costa Rica"). *Tantilla melanocephala* has been considered to have 2 subspecies, *T. m. melanocephala* and *T. m. capistrata* (the latter was described as a distinct species by Cope, 1876*b*, from a specimen from the valley of Jequetepeque, Perú).

Most of these nominal species agree with one another in possessing a dark middorsal stripe, generally confined to the middorsal scale row (absent in some specimens of *T. capistrata* and *T. melanocephala*), a dark head cap separated from a dark nape band by a pair of variously-sized nuchal spots or a complete or medially divided nuchal band (dark nape band absent in one species). Some specimens from Amazonian South America and northwestern Perú lack a middorsal stripe. In such cases, however, the head pattern is the same as in striped specimens from the same or surrounding areas. There are also present a pale preocular and postocular spots separated by a dark subocular blotch. All members have 7 supralabials and 2 postoculars. Most members have a pale lateral stripe (except *T. capistrata* and some *T. melanocephala*).

Study of material of this group has demonstrated that all the nominal taxa of this group listed above (except *T. capistrata*) are actually part of one wide-ranging variable species. Recent collections, however, have demonstrated the presence of additional new species, which are described below.

Species Discrimination in the *melanocephala* Group

In this study, we divided the available material into several groups on the basis of color pattern. Eleven distinct color patterns were thus discriminated (see diagnoses below). Some of these patterns could be associated with that described for certain nominal species (*T. armillata*, *T. fraseri*, *T. longifrontalis*, and *T. ruficeps*) or subspecies (*T. capistrata*) and others appeared to belong to undescribed taxa. In the absence of type material, the pattern characteristics of *T. melanocephala* (sensu stricto) could not be determined. This problem proved unimportant as all of the above taxa (except *T. capistrata*) are part of a single variable and widely distributed species for which the name *T. melanocephala* is used (see reasoning below). An additional currently recognized nominal taxon (*T. mexicana*) proved to be based on a specimen not exhibiting a unique color pattern and having an incorrect type locality.

The next step of the discrimination analysis involved examination of the material of the various color pattern types for evidence of sympatry or intergradation. No evidence of sympatry was found but evidence of intergradation was and this evidence is used in defining species limits.

Using this approach, the pattern that emerged was one involving a wide-ranging species (*T. melanocephala*) occurring from Guatemala to Argentina within which 6 distinct color pattern assemblages (2 of which are sympatric with one another) could be identified. Most of these color pattern types have formed the basis in the past for the recognition of species-level taxa within the *melanocephala* group. One currently-recognized name (*T. longifrontalis*) proved to be based on material from a population intergradient between pattern types within *T. melanocephala*.

Additional satellite species not connected to the wide-ranging *T. melanocephala* by intergradation were found to occur in lowland and highland locales in Ecuador, in lowland coastal habitats in northwestern Perú, and in the pine uplands of south-central Honduras.

The *Tantilla melanocephala* Population System

Color pattern has proved to be the key to unraveling relationships within the *T. melanocephala* population system. And, indeed, characteristics of pattern have been used in the past to diagnose the species-level taxa that are herein

considered to be part of *T. melanocephala*. On the basis of pattern, the *T. melanocephala* population system can be seen to be composed of 5 units that show geographical integrity. For purposes of analysis one of these units is considered to house 2 pattern morphs, a striped and nonstriped form. The ranges of these population units are described in the discussion of color pattern types below. Intergradation between populations, as defined by intermediacy between color pattern types, as well as in certain scutellational characters, is also discussed below. Discussion of variation in scutellation follows the discussion of color pattern types.

Color Pattern.—There are 6 separate identifiable patterns within the species *T. melanocephala* which show varying degrees of geographical integrity and most of which have formed the basis for the recognition of taxa. These 6 patterns are described as follows (species name, if any, applied to the pattern types indicated in parentheses):

(1) pattern A ("*armillata*")—this pattern (Figs. 1, 6A), which is found in specimens from principally along the Pacific versant (Atlantic versant in Honduras, Nicaragua, and Costa Rica) from Guatemala to northern Costa Rica (Fig. 15), is characterized by: (a) a dark brown head cap (89.4% of specimens), with usually a small amount of pale pigment on the anterior or anteromedial portion of the internasals and pale spots near the junction of the supraocular, frontal, and parietal; (b) a pair of small, pale nuchal spots, usually located on the posterior portion of the parietals (82.6% of specimens), but sometimes extending also onto a small portion of the posterior temporal and/or adjacent postparietal scale (17.4%); (c) a dark brown nape band 3½-6 middorsal scales long ($\bar{x}=4.9$); (d) tan (56.3% of specimens), pale brown (33.3%), or brown (10.4%) ground color, with narrow dark brown middorsal stripe confined to middorsal scale row; (e) dark subocular blotch completely separating (41.9% of specimens) preocular and postocular pale spots or not (58.9%); (f) lateral extension of dark head cap usually present, separating the postocular pale spot from the pale pigment on the lateral gulars (opposite the pale nuchal spots) completely (55.3% of specimens) or not (44.7%); (g) pale neck band following the dark nape band ½-2 scales in length ($\bar{x}=1.1$), in turn bounded posteriorly by a series of dark brown spots (91.7% of specimens); (h) pale lateral band usually poorly indicated, occupying the upper half of row 3 and the lower half of 4, but frequently absent (31.9% of specimens)—specimens from Honduras show a high incidence of a lack of a pale lateral stripe (83.3%), as opposed to the other countries (14.3%), if present, not bounded by dark pigment.

(2) pattern B ("*ruficeps*")—this pattern (Figs. 2, 6B), which is found in specimens from principally along the Atlantic versant (Pacific versant in Costa Rica) in Nicaragua (exact locality and versant unknown), Costa Rica, and extreme western Panama (Fig. 15), is characterized by: (a) a tan (11.1% of specimens), pale brown (77.7%), or brown (11.2%) head cap, with no pale pigment on snout; (b) an inconspicuous pair of pale nuchal spots (on posterior portion of parietals and a portion of the posttemporal and adjacent postparietal scales), if present (not present in 55.5% of specimens); (c) a brown to dark brown nape band 3-6 middorsal scales long ($\bar{x}=4.6$), sometimes absent (11.1% of specimens); (d) tan (22.2% of specimens), pale brown (11.1%), or brown (66.7%) ground color, with well-developed dark brown middorsal stripe confined to middorsal scale row; (e) dark subocular blotch, if present, poorly developed, consisting of dark pigment along suture lines between supralabials 3, 4, and 5; (f) lateral extension of dark head cap usually absent (66.7% of specimens), but sometimes present (33.3%) and completely separating the postocular pale spot from the pale pigment on the lateral gulars (opposite the pale nuchal spots, if the latter are present); (g) pale neck band following the dark nape band absent; (h) pale lateral band always present, well-developed and contrasting well with surrounding color, occupying from as little as the upper half of row 3 and the lower half of row 4 (22.2% of specimens) to as much as the upper half of row 3, all of row 4, and the lower half of row 5 (44.5%)—33.3% of specimens have the stripe occupying the upper half of row 3 and all of row 4, and bounded above and below by dark brown pigment.

(3) pattern C (stripeless pattern): this pattern, which is found in southeastern Colombia, Venezuela, Bolivia, Brazil, British West Indies, and Argentina (Fig. 14), is characterized by: (a) a cream (2.1% of specimens), pale brown (16.7%), brown (47.9%), or dark brown (33.3%) head cap, with usually pale pigment on the internasals and frequently also on the prefrontals; (b) nuchal band complete (2.0% of specimens), divided medially only (22.4%), or divided both medially and laterally (75.6%), when the latter the nuchal spots are present only on the posterior portion of the

parietal (19.4% of specimens), on the posterior portion of the parietals and adjacent portion of the posterior temporal (3.2%), on the parietals, posterior temporal and a portion of 1 adjacent postparietal scale (58.1%), on the parietals, posterior temporal and portions of 2 adjacent postparietal scales (12.9%), or on the parietal, posterior temporal and adjacent portions of 3 adjacent postparietal scales (6.4%); (c) an usually dark brown nape band 3-7 middorsal scales long ($\bar{x}$ =3.9); (d) tan (72.9% of specimens), pale brown (12.5%), or brown (14.6%) ground color, with a middorsal dark stripe; (e) dark subocular blotch touching lip (46.0% of specimens) or not (54.0%); (f) lateral extension of dark head cap usually present and touching lip (80.4% of specimens), but sometimes not (19.6%); (g) pale neck band following dark nape band usually present (82.0% of specimens), measuring ½-1½ middorsal scales in length ($\bar{x}$ =.78), not bounded posteriorly by dark pigment; (h) pale lateral band usually absent (96.0% of specimens), but present in a few (4.0%), when present, not bounded by dark pigment.

(4) pattern D (eastern South America): this pattern (Figs. 3, 6C), which is found in southeastern Colombia, Venezuela, Bolivia, Brazil, British West Indies, Surinam, Guyana, Paraguay, Uruguay, and Argentina (Fig. 14), is characterized by: (a) a pale brown (16.1% of specimens), brown (67.8%), or dark brown (16.1%) head cap, with usually pale pigment on the internasals and frequently also on the prefrontals; (b) nuchal band divided medially only (19.2% of specimens) or divided both medially and laterally (80.8%), when the latter, the nuchal spots are present only on the posterior portion of the parietal (13.5% of specimens), on the posterior portion of the parietals and adjacent portion of the posterior temporal (2.7%), on the parietal, posterior temporal and a portion of 1 adjacent postparietal scale (70.3%), on the parietals, posterior temporal and portions of 2 adjacent postparietal scales (8.1%), or on the parietal, posterior temporal and portions of 3 adjacent postparietal scales (5.4%); (c) an usually dark brown nape band 2-5 middorsal scales long ($\bar{x}$ =3.6); (d) tan (50.0% of specimens), pale brown (24.1%), or brown (25.9%) ground color, with a usually diffuse and oftentimes brown dark middorsal stripe confined to the middorsal scale row; (e) dark subocular blotch touching lip (40.0% of specimens) or not (60.0%); (f) lateral extension of dark head cap usually present and touching lip (76.4% of specimens), but sometimes not (23.6%); (g) pale neck band following dark nape band usually present (62.5% of specimens), measuring ½-1½ middorsal scales in length ($\bar{x}$ =.90), not bounded posteriorly by dark pigment; (h) pale lateral band usually absent (63.0% of specimens), but often present (37.0%), in which case the stripe usually (75.0%) occupies the upper half of row 3 and all of row 4.

(5) pattern E (Amazonian Ecuador and Perú): this pattern (Figs. 4, 6D), which is found in the Amazonian drainage of Ecuador and Perú (Fig. 14), is characterized by: (a) a pale brown (1.4% of specimens), brown (95.8%), or dark brown (2.8%) head cap, with usually pale pigment on the internasals and prefrontals; (b) nuchal band divided medially only (21.3% of specimens) or divided both medially and laterally (78.7%), when the latter the nuchal spots are present on the posterior portion of the parietals and an adjacent portion of the posterior temporal (1.8% of specimens), on the parietal, posterior temporal and a portion of 1 adjacent postparietal scale (49.1%), on the parietal, posterior temporal, and portions of 2 adjacent postparietal scales (41.8%), or on the parietal, posterior temporal, and adjacent portions of 3 adjacent postparietal scales (7.3%); (c) an usually dark brown nape band 3-5 middorsal scales long ($\bar{x}$ =3.7); (d) tan (2.5% of specimens), pale brown (23.5%), or brown (74.0%) ground color, with a well-developed, complete dark middorsal stripe confined to the middorsal scale row; (e) dark subocular blotch touching lip (88.9% of specimens) or not (11.1%); (f) lateral extension of dark head cap usually present and touching lip (97.6% of specimens), but sometimes not (2.4%); (g) pale neck band following dark nape band usually present (93.8% of specimens), measuring ½-2 middorsal scales in length ($\bar{x}$ =1.0), not bounded posteriorly by dark pigment; (h) pale lateral band usually present (96.3% of specimens), in which case the stripe occupies only the upper portion of row 3 (17.4% of specimens), the upper half of row 3 to the middle of row 4 (8.1%), the upper half of row 3 and all of row 4 (58.1%), or the upper half of row 3 through the lower half of row 5 (16.4%), but sometimes absent (3.7%), bounded by dark pigment.

(6) pattern F ("*fraseri*"): this pattern (Figs. 5, 6E), which is distributed along the western slopes of the Andes in Ecuador (Fig. 14), is characterized by: (a) a brown head cap, with usually no pale pigment on snout (60.0% of specimens), if present, however, usually occupying all of the internasals and the anterior one-third to almost all of the internasals; (b) nuchal band divided medially and

Table 1. Primary distinctions between the color pattern types in *Tantilla melanocephala*.

Characters	Color pattern types					
	A	B	C	D	E	F
1. Ground color of dorsum of head	Dark brown	Pale brown	Brown to dark brown	Brown	Brown	Brown
2. Pale pigment on internasals and prefrontals	No	No	Yes	Yes	Yes	No
3. Pale nuchal spots	Restricted to parietal scales	Not present or present and divided medially and laterally	Divided medially and laterally	Divided medially and laterally	Divided medially or medially and laterally	Divided medially and laterally
4. Color of dark nape band	Dark brown	Brown to dark brown	Dark brown	Dark brown	Dark brown	Brown
5. Mean length of dark nape band	4.9	4.6	3.9	3.6	3.7	4.1
6. Lateral extension of dark head cap present and touching lip	Yes	No	Yes	Yes	Yes	Yes
7. Pale neck band present	Yes	No	Yes	Yes	Yes	Yes
8. Mean length of pale neck band	1.1	...	.78	.90	1.0	.78
9. Pale neck band bounded posteriorly by dark pigment	Yes	No	No	No	No	No
10. Ground color of dorsum of body	Tan to pale brown	Brown	Tan	Tan to brown	Brown	Brown
11. Middorsal dark stripe present	Yes	Yes	No	Yes, diffuse and broken	Yes	Yes
12. Pale lateral band	Present or absent, but if present, poorly indicated	Present	Absent	Absent	Present	Present
13. Area covered by pale lateral band	Upper half of row 3 and lower half of 4	Upper half of row 3 through all of row 4 or lower half of row 5	...	...	Upper half of row 3 to upper half of row 4 through lower half of row 5	Upper half of row 3 to middle of row 4 through lower half of row 5
14. Pale lateral stripe bounded by dark pigment	No	Yes	No	No	Yes	Yes

laterally, the nuchal spots covering the posterior portion of the parietal and a portion of the adjacent posterior temporal (6.3% of specimens), the parietal, posterior temporal, and a portion of 1 adjacent postparietal scale (62.5%), the parietal, posterior temporal, and a portion of 2 adjacent postparietals (12.5%), or the parietal, posterior temporal, and portions of 3 adjacent postparietals (18.7%); (c) an usually brown nape band 3-5 middorsal scales long ($\bar{x}=4.1$); (d) pale brown (17.6% of specimens) or brown (82.4%) ground color, with a well-developed, complete dark middorsal stripe confined to the middorsal scale row; (e) dark subocular blotch touching lip (80.0% of

specimens) or not (20.0%); (f) lateral extension of dark head cap usually present and touching lip (70.6% of specimens), but sometimes not (29.4%); (g) pale neck band following dark nape band usually present (75.0% of specimens), sometimes confined to one or two scales on either side of the dark middorsal stripe, when complete, measuring ½-1 middorsal scales in length ($\bar{x}$=.78), but sometimes absent (25.0%), not bounded posteriorly by dark pigment; (h) pale lateral band usually present (94.1% of specimens), in which case the stripe occupies only the upper portion of row 3 (6.1% of specimens), the upper half of row 3 through the middle of row 4 (31.3%), the upper half of row 3 and all of row 4 (31.3%), or the upper half of row 3 through the lower half of row 5 (31.3%), but sometimes absent (5.9%), bounded by dark pigment.

The primary distinctions between the color pattern types in *Tantilla melanocephala* are summarized in Table 1. The characteristics listed in that table are the mean or modal characteristics, not the range of characteristics exhibited in each pattern type.

Two things are evident from a perusal of the above pattern diagnoses. One, that most of Panama and all of Colombia have not been included in any of the range statements for the various pattern types. This is because we consider this area to be one of integradation between patterns A and B to the north and patterns C, D, E, and F to the south and east. This intergradation is discussed in more detail below. Secondly, patterns C and D are, in large part, sympatric; actually, they grade into one another and are separated purely for the sake of convenience.

When we first began to study the *melanocephala* group, we were perplexed by the material from Panamá, which resembled the nominal species *T. armillata* in pattern, but the nominal species *T. ruficeps* in ventral and subcaudal counts. As the study progressed, however, it became clear that the Panamanian material was intermediate and, in fact, intergradient between nominal *T. armillata* (pattern A) and nominal *T. ruficeps* (pattern B). A comparison between the 3 groups of specimens is made in Table 2. The mean or modal condition of each character is listed in this table. As can be seen from the table, Panamanian specimens agree more closely in pattern with the members of pattern A than with those of pattern B. Panamanian specimens agree with members of pattern A in the nature and extent of the pale neck band, the presence of dark pigment posterior to the pale neck band, the dorsal ground color, and the lack of dark pigment on the venter. The resemblance between the two in pattern and their distinction from that of the members of pattern B is immediately apparent. Panamanian specimens resemble the members of pattern B in the area covered by the pale nuchal spots (if present in the latter), the mean length of the dark nape band, and the presence of dark pigment on the lateral dorsum (more extensive in the latter). Panamanian specimens exhibit an intermediate head color.

The picture in Colombia was initially even more confused, but again, as the study progressed, it became apparent that most of Colombia is an area of intergradation between members of pattern types C and D, E, and F. Also, the same type of pattern seen in Panamanian specimens is also seen in specimens from parts of Colombia.

To elucidate pattern variation in Colombia, we divided the material into several geographic groupings: (a) Pacific coastal region; (b) Atlantic coastal region; (c) Cordillera Occidental; (d) Cordillera Central; (e) Cordillera Oriental; (f) Amazonian region. Data on pattern characteristics for these groupings were then compared to those for members of pattern groups C, D, E and F. The summarization follows:

(1) Pacific coastal region.—The few specimens available from this region all resemble the Panamanian specimens in pattern. The Pacific coastal specimens primarily have a brown head cap with the nuchal spots covering the posterior portion of the parietals and a portion of the posterior temporal and one adjacent postparietal scale, an average dark nape band length of 4.0 scales, pale pigment on all of the internasals and the anterior one-fourth to one-half of the prefrontals, an average pale neck band length of 1.3 scales, pale lateral band covering from the upper half of row 3 through all of row 4 to the upper half of row 3 through the lower half of row 5, dark pigment on lower dorsum occupying the upper half of row 2 and the lower half of row 3, a tan to pale brown ground color, and no dark pigment on the venter.

(2) Atlantic coastal region.—The 3 specimens from this area are all unalike. One specimen (UMMZ 54957) from Depto. Magdalena resembles specimens from adjacent Panama. A second (FMNH 165193) from Depto. Bolívar strongly resembles specimens from Central America (Guatemala to Costa Rica-pattern A), especially in head pattern (small parietal spots,

Table 2. Comparison of color pattern characteristics among pattern A, pattern B, and Panamanian specimens.

Characters	Pattern A	Panamanian Specimens	Pattern B
Ground color of dorsum of head	Dark brown	Brown	Pale brown
Area covered by pale nuchal band	Posterior portion of parietals	Posterior portion of parietal and adjacent portions of posterior temporal and one postparietal	Absent or poorly indicated on posterior portions of parietal, posterior temporal, and adjacent postparietal
Length of dark nape band	4.9	4.6	4.6
Color of dark nape band	Dark brown	Dark brown	Dark brown
Amount of pale pigment on snout	Anterior ⅓ of internasals	Anterior ⅔-¾ of internasals and ¼-⅓ of prefrontals	Absent
Area covered by pale neck band	1 scale length	1 scale length	1 or 2 scales on either side of middorsal line
Dark pigment posterior to pale neck band	Present	Present	Absent
Area covered by pale lateral stripe	Absent or barely indicated on upper half of row 3 and lower half of row 4	Upper half of row 3 and all of row 4	Well-distinguished, ranges from upper half of row 3 through lower half of row 4 to upper half of row 3, all of row 4, and lower half of row 5
Dark pigment on lateral dorsum	Absent	Present	Present
Ground color of dorsum of body	Tan to pale brown	Tan to pale brown	Brown
Dark pigment on venter	Absent	Absent	Present

ground color of dorsum of head and dark nape band the same, well-defined pale neck band, and band of dark pigment posterior to pale neck band) and lack of pale lateral stripe. The dark middorsal stripe is barely discernible, however. The locality data for this specimen could be incorrect and the specimen actually could be from Central America, but the nature of the middorsal stripe and other scutellational features discussed below casts that decision in doubt. This particular area needs further investigation, as does the whole of the Atlantic coastal region of Colombia. A third specimen (NMW 20367) from Depto. Atlántico resembles that of pattern C specimens in all respects, which is to be expected considering the proximity of its locality to Venezuela, one of the countries in which pattern C specimens are found.

(3) Cordillera Occidental.—The 3 specimens from this area are in relatively poor shape and their affinities are difficult to judge. A perusal of their pattern characteristics allies them most closely with pattern E specimens. This area is also in need of further study.

(4) Cordillera Central.—Eighteen specimens are available from this area. Ten specimens show resemblance to specimens from Panamá, 3 to pattern F specimens, 2 to pattern E specimens, and 3 are intermediate between specimens from Panamá and pattern F specimens. Most specimens from this area are from Depto. Antioquia, which appears to be an area of integradation between Panamanian specimens (which are themselves intergradient) and pattern F specimens. Two specimens from deptos. Caldas and Cauca

resemble pattern E specimens.

(5) Cordillera Oriental.—Specimens from this area resemble either Panamanian specimens or pattern E specimens. The few specimens available (5) do not give a clear picture of variation in color pattern and additional material is to be desired.

(6) Amazonian region.—Specimens from this area resemble either specimens from Panamá (UTACV 3476 from Depto. Meta), pattern C or D specimens (MCZ 53236 and UTACV 3535 from Depto. Vaupés and UTACV 3717 from Depto. Meta), or pattern E specimens (MCZ 49003 from Depto. Amazonas and FMNH 37448 from Depto. Putamayo). These relationsips make geographic sense as deptos. Putamaya and Amazonas are close to the Amazonian lowlands of Ecuador and Perú, where pattern E specimens are found and deptos. Meta and Vaupés are close to Venezuela and Brazil from which area pattern C and D specimens are found. This area will, no doubt, prove to be one of intergradation between Panamanian specimens, pattern E specimens, and pattern C and D specimens, when more material becomes available.

On the basis of color pattern, the entire country of Colombia is one in which there is a meeting and, in many cases, a merging of pattern elements from the north (pattern of Panamanian specimens), east (patterns C and D), southeast (pattern E) and south (pattern F). It is primarily upon this evidence that we consider members of the pattern types discussed above (patterns A-F) to constitute a single species. Pattern A and B specimens in Central America intergrade with one another in Panamá. The Panamanian intergradient pattern extends into Colombia where it meets or merges with the patterns found in South America (patterns C-F).

In summary, 6 pattern types that occupy 5 distinct geographic areas are present within the *Tantilla melanocephala* population system. The status of the various names associated with these pattern types is discussed below. Intergradation in color pattern has been shown to occur in Panamá and Colombia between patterns A and B to the north in Central America and patterns D-D, E and F to the south and east in the remainder of the range of the population system in South America.

Ventrals.—Ventral numbers in the *Tantilla melanocephala* population system range from 125-174 in males and 134-177 in females. The highest counts for males and females are for specimens from Honduras; the lowest are for specimens from the department of Junín in Perú. The mean values follow the same pattern, except that the lowest mean for females is for specimens from the Cordillera Oriental of Colombia (139.0), followed closely by the mean (141.6) for females from the eastern slopes of the Andes in Perú (within which area lies the department of Junín).

As indicated in Table 3, where the sample size is large enough, females have more ventrals than males ($\bar{x}=7.5$).

Ventral numbers are highest in Central America from Guatemala to northwestern and central Costa Rica. In this area, ventrals range in males from 155 to 174 and in females from 158 to 177. The numbers appear to be relatively low in Guatemala and El Salvador and they increase in Honduras. They drop again in western Nicaragua and become elevated again in northwestern and central Costa Rica.

The ventral numbers drop dramatically on the Altantic slope and southwestern Pacific slope of Costa Rica and this trend continues on into Panamá. Compared to numbers in northwestern and central Costa Rica, there is over a 20-scale drop in mean ventral number in the area in Costa Rica mentioned above. Ventral numbers are similar in Panamá to those in Costa Rica. Ventral range in these lower Central American specimens is from 139 to 149 in males and 143 to 155 in females. There is no range overlap between these specimens and those from upper Central America (northwestern Costa Rica north).

The numbers increase again in Colombia (except in the Cordillera Oriental). The range for Colombia (exclusive of the Cordillera Oriental) is from 136 to 165 ($\bar{x}=150.9$) for males and 146 to 169 ($\bar{x}=158.4$) for females. The specimens from the Cordillera Oriental in Colombia have incongruously low numbers of ventrals. The range for males is 127-148 ($\bar{x}=136.0$) and for females 135-143 ($\bar{x}=139.0$). The means are ≈ 15 scales higher in other parts of Colombia than in the Cordillera Oriental. This is interpreted as evidencing influence from the Amazonian region of Ecuador where ventral numbers are low as well (see below).

In Venezuela, ventral numbers are relatively low in the Cordillera Mérida (the continuation of the Cordillera Oriental of Colombia into Venezuela). In other areas, however, numbers are higher, ranging from 142-162 ($\bar{x}=153.7$) in males and 147-167 ($\bar{x}=159.2$) in females, as compared to a count of 144 in one male and a range of 142-150 ($\bar{x}=145.8$) in females.

Table 3. Variation in the numbers of ventrals and subcaudals in *Tantilla melanocephala* (range, $\bar{x}$, *N*).

Geographic area	Ventrals		Subcaudals	
	♂♂	♀♀	♂♂	♀♀
Southern Guatemala	...	160-173(166.5)2	...	44(44.0)2
Central El Salvador[1]	166-172(168.3)3	170	46-54(50.7)3	45
Honduras	170-174(172.0)2	168-177(171.1)12	54	42-60(47.8)10
Western Nicaragua	155-166(161.0)6	158-173(165.9)9	50-56(53.0)5	44-51(46.6)7
Eastern(?) Nicaragua[2]	...	148	...	59
Pacific slope of northwestern and central Costa Rica	163-167(164.9)7	169-174(170.9)7	51-59(55.8)6	48-52(50.0)4
Atlantic slope and southwestern Pacific slope of Costa Rica	142-148(144.3)4	144-147(145.5)2	64-77(69.7)3	66-75(70.5)2
Western Panamá	144	143-155(149.0)2	82	63-68(65.5)2
Central and eastern Panamá	139-149(143.5)12	143-154(152.0)10	69-79(75.1)10	66-71(68.3)8
Pacific coastal region of Colombia	159	157-169(164.0)3	...	70-74(72.0)2
Atlantic coastal region of Colombia	...	150-162(157.7)3	...	55-72(63.5)2
Cordillera Occidental of Colombia	147	160	61	...
Cordillera Central of Colombia	136-158(150.9)9	146-168(157.3)8	62-92(74.5)6	52-72(64.6)7
Cordillera Oriental of Colombia	127-148(136.0)3	135-143(139.0)2	58-80(71.3)3	55
Amazonian region of Colombia	141-165(150.0)5	152-157(154.5)2	56-69(62.5)4	46
Cordillera de Mérida of Venezuela	144	142-150(145.8)4	63	54-56(55.0)2
Caribbean coastal plain of Venezuela	159	154-162(158.0)5	65	53-56(55.0)4
Cordillera de la Costa of Venezuela	142-162(152.6)5	147-167(160.0)7	61-76(66.4)5	53-68(57.8)6
Guiana highlands of Venezuela	...	149-157(153.7)3	...	53-58(55.5)2
Monaguesa formation of Venezuela	...	152	...	...
Trinidad	137-152(138.8)7	147-159(150.7)13	59-67(63.0)5	47-60(54.5)11
Tobago	157-160(159.0)3	168	73-79(76.0)3	68
Guyana	133-144(136.8)9	140-158(147.3)4	50-66(57.6)7	66
Surinam	139-140(139.5)2	...	61	...
Brazil	136-154(143.4)7	141-155(147.9)7	56-63(59.8)6	55-56(55.5)2
Uruguay	...	155	...	...
Paraguay	144	...	...	...
Argentina	158	167	68	60
Bolivia	126-151(140.0)6	158-165(161.5)2	49-62(55.2)5	49-55(52.0)2
Coastal plain of Ecuador	141-142(141.5)2	...	50-65(57.5)2	...
Western slopes of Andes in Ecuador	136-147(142.3)9	144-154(149.6)7	51-72(61.3)7	58-65(62.0)4
Inter-Andean basins of Ecuador (Pacific drainage)	...	156-158(157.0)2	...	55-58(56.5)2
Inter-Andean basins of Ecuador (Atlantic drainage)	136	142	59	...
Oriente of Ecuador	134-145(138.0)17	139-150(144.5)8	54-58(56.4)10	51-57(53.3)4
Andean Cordillera in Perú	134-136(135.0)2	143	47	...
East Andean slopes in Perú	125-143(133.9)11	134-153(141.6)12	46-53(49.5)8	41-63(49.1)7
Tropical lowlands of Perú	136-159(144.0)21	142-152(148.4)7	41-62(50.9)16	44-50(46.5)6

[1]Data on 3 of 4 specimens from this area are from Mertens (1952*a*).
[2]Locality uncertain, but specimen thought to be from eastern Nicaragua.

Variation in ventrals in the British West Indies presents an interesting picture. Trinidad is 18 to 19 kilometres from the nearest point on the mainland of Venezuela in the north and ≈ 13 kilometres in the south (across the delta of the Orinoco River) and Tobago is 28 to 29 kilometres from the nearest point on Trinidad (near Toco). The differences in ventral counts between specimens from Trinidad and adjacent Venezuela, compared to specimens from Trinidad and Tobago, are striking. Mean ventral numbers in Trinidad are lower by approximately 8 to 15 scales than specimens from adjacent Venezuela. On Tobago, ventral numbers again increase markedly over those in Trinidad and are even higher than those from mainland Venezuela. In fact, only specimens from upper Central America have higher ventrals than those of specimens from Tobago. The mean for ventrals for Trinidad males is 20.2 scales lower than that for Tobagan males. Comparable figures for females are not available, but the count for the single Tobagan female is 9 scales above the highest count for Trinidad females.

Ventral numbers decrease in the Guianas (material available only from Guyana and Surinam) as compared to adjacent areas in Venezuela, as well as in Brazil, Uruguay and Paraguay, but increase again in Argentina (the pattern in the latter 4 countries is poorly understood due to the paucity of material).

Variation in ventrals in males from Bolivia is similar to that in other parts of eastern South America. Females from Bolivia (only 2 specimens are available), however, have much higher ventral counts than those of specimens from eastern South America and are closer to those from the Cordillera de la Costa of Venezuela. In addition, the range in Bolivian males (126-151) is the widest of any of that in any of the areas within the range.

Ventral numbers decrease in Ecuador and Perú, compared to those in Colombia (exclusive of the Cordillera Oriental). Within this area, however, there are additional patterns worthy of notice. Specimens from the Pacific coastal plain, western Andean slopes, and the inter-Andean basins of Ecuador (Pacific drainage) have more ventrals than those from the Atlantic drainage inter-Andean basins and the Amazonian lowlands of Ecuador (means of 142.2 and 149.6 in males and females, respectively, in the former and 137.9 and 144.2 in the latter). The numbers of ventrals for specimens from the Andean cordillera and the eastern Andean slopes in Perú are similar to those from the Amazon drainage of Ecuador, but those from the Amazonian lowlands of Perú are higher.

Subcaudals.—Subcaudal numbers in the *Tantilla melanocephala* population system range from 41-92 in males and 41-75 in females. The highest count for males is that for a specimen from the Cordillera Central of Colombia and for females a specimen from the southwestern Pacific slope of Costa Rica. The lowest count for males is for a specimen from the tropical lowlands of Perú and for females a specimen from the eastern slopes of the Andes in Perú. The mean values do not show the same pattern, probably primarily due to atypically high counts being represented in small samples.

As can be seen in Table 3, where sample sizes are large enough, males have more subcaudals than females ($\bar{x}=4.3$).

Subcaudal numbers are the lowest anywhere within the population system (with the exception of the eastern Andean slopes and tropical lowlands of Perú, where the numbers are about the same as they are in Central America) in Central America from Guatemala to northwestern and central Costa Rica. In this area, subcaudals range in males from 46-59 and in females from 42-60. The subcaudal numbers appear to increase gradually within this area from north to south.

The subcaudal numbers increase markedly on the Atlantic slope and southwestern Pacific slope of Costa Rica and this trend continues on into Panamá. Compared to numbers in northwestern and central Costa Rica, there is a 14-20 scale increase in mean subcaudal number in the area of Costa Rica mentioned above. Subcaudal numbers in Panamá are similar to those in the area of Costa Rica under discussion. Subcaudals range in these lower Central America specimens from 64-82 in males and 63-75 in females and there is no overlap of these ranges with those for specimens from upper Central America.

Subcaudal numbers vary widely in Colombia. Mean numbers for specimens from the Pacific coastal region, the Cordillera Central, and the Cordillera Oriental are similar to those of specimens from Panamá but the ranges are much wider (58-92 in males and 52-74 in females, as compared to 69-82 and 63-71). Numbers for specimens from the Atlantic coastal region and the Amazonian region are lower than those for specimens from other areas of Colombia and those from Panamá.

Subcaudal numbers are relatively low in

Table 4. Variation in contact of prefrontal and second supralabial in *Tantilla melanocephala*.

Geographic area	*N*	Contact		
		None	One side	Both sides
Guatemala	2	...	...	2
El Salvador	4	...	...	4
Honduras	13	...	1	12
Nicaragua	16	...	...	16
Costa Rica	20	3	1	16
Panamá	30	...	...	30
Colombia	39	5	...	34
Venezuela	36	9	3	24
Trinidad	20	2	1	17
Tobago	4	1	...	3
Guayana	13	8	...	5
Surinam	2	2	...	...
Brazil	14	10	...	4
Argentina	2	...	...	2
Uruguay	1	...	...	1
Paraguay	1	1	...	...
Bolivia	8	3	3	2
Perú	59	37	3	19
Ecuador	53	16	5	32

Venezuela and Trinidad, although not as low as they are in upper Central America. The ranges for all of Venezuela and Trinidad are 59-76 for males and 47-68 for females.

As with ventrals, variation in subcaudals in the British West Indies is interesting. The mean for subcaudals for Trinidad males is 13 scales lower than that for Tobagan males. Although a comparable figure is not available for females, the count for the single Tobagan female is 8 scales above the highest count for Trinidad females.

Subcaudal numbers in the Guianas, Brazil and Argentina are similar to those in Venezuela, as best as can be demonstrated with the small samples from these countries.

Specimens from Bolivia have lower numbers of subcaudals than other specimens from eastern South America in both males and females.

Subcaudal numbers decrease in Ecuador, as compared to those for specimens from Colombia. Within Ecuador subcaudal numbers are higher for specimens west of the Continental Divide than for those east of it (means of 60.5 and 60.2 in males and females, respectively, in the former and 56.6 and 53.3 in the latter).

Subcaudal numbers continue to decrease in Perú, as compared with eastern Ecuador and average 5-6 scales lower.

Anal plate.—All specimens examined have a divided anal plate (as is characteristic of the genus *Tantilla*) except 2 specimens, one from Panamá and another from Colombia.

Dorsal scale rows.—All specimens examined have 15 dorsal scale rows throughout (which is characteristic of *Tantilla*) except for 2 specimens. One specimen from Bolivia has 13 scale rows on the neck and another from Perú has 17 scale rows at midbody and at the vent.

Supralabials.—All specimens have 7 supralabials, with the 3rd and 4th entering the orbit, with a very few exceptions. Five specimens have 6-7 supralabials, one has 5-7 (supralabials 5, 6 and 7 fused on left side), and one has 7-8. All specimens showing the variances are from South America, albeit from widely divergent localities.

Infralabials.—The majority of the specimens examined (92.8%) have 6 infralabials, with 4 in contact with the anterior chin shields and the 4th the largest. The range in infralabial number, however, is 4-7 and as few as 3 or as many as 5 infralabials may be in contact with the anterior chin shields.

Contact of prefrontal and second supralabial.—This character has frequently been used as a distinguishing feature between species of *Tantilla* and the *melanocephala* group is no excep-

Table 5. Variation in medial contact of first pair of infralabials in *Tantilla melanocephala.*

Geographic area	*N*	Medial contact	
		Absent	Present
Guatemala	1	...	1
El Salvador	4	...	4
Honduras	13	4	9
Nicaragua	16	2	14
Costa Rica	20	2	18
Panamá	30	1	29
Colombia	40	8	32
Venezuela	35	...	35
Trinidad	20	...	20
Tobago	4	...	4
Guayana	13	2	11
Surinam	2	...	2
Brazil	14	2	12
Argentina	2	...	2
Uruguay	1	...	1
Paraguay	1	...	1
Bolivia	8	2	6
Perú	59	28	31
Ecuador	53	14	39

tion (see Peters and Orejas-Miranda, 1970: 293).

The pattern of variation in this character (Table 4) does not support its use as a species or subspecies distinguishing characteristic. Most specimens from Central America, Colombia, Venezuela and the British West Indies (85.9%) have the prefrontal and second supralabial in contact on both sides of the head, separating the postnasal and preocular scales. Conversely, a large percentage of specimens from Guyana, Surinam, Brazil, Paraguay, Bolivia, and Perú (62.9%) have no contact between the prefrontal and second supralabial. The pattern in Uruguay and Argentina is not clear but available material agrees with the condition in the northern segment of the range. Specimens from Ecuador are, to some extent, intermediate between those to the north and those to the south. They agree with specimens to the north in having the highest percentage of specimens showing contact between the prefrontal and second supralabial on both sides, although the percentage is considerably lower than in adjacent Colombia (87.2%), for example. Ecuadoran specimens showing no contact constitute 30.2% of the sample, a figure intermediate between that for Perú (62.7%) and that for Colombia (12.8%).

Medial contact of first pair of infralabials.—In most portions of the *T. melanocephala* population system the infralabials of the first pair are in medial contact (Table 5) in the majority of specimens (89.7%), but in Perú and Ecuador this percentage drops to 62.5 and a corresponding 37.5% of the specimens have the first pair of infralabials separated. In fact, in Perú the percentages are almost equal to one another (52.5% with medial contact, 47.5% without) and specimens are intermediate between those from Perú and those from the remainder of the range. Variation in this character also does not support its use as a species or subspecies distinguishing characteristic.

Preoculars.—All specimens examined, except 4, have a single preocular on both sides of the head. Three specimens, one each from Nicaragua, Tobago, and Perú, have no preocular on one side of the head and one specimen from Costa Rica has 2 on both sides.

Postoculars.—All specimens examined, except 5, have 2 postoculars on both sides of the head. Two specimens, one from Perú, the other from Venezuela, have but a single postocular on one side. A specimen from Guyana has the lower postocular fused with the 4th supralabial; another from Perú has it fused with the 5th supralabial.

Table 6. Variation in relative tail length in *Tantilla melanocephala*.

Geographic area	Relative tail length	
	♂♂	♀♀
Southern Guatemala	...	0.179-0.182(0.181)2
Central El Salvador	0.210	...
Honduras	0.205	0.181-0.202(0.190)8
Western Nicaragua	0.180-0.229(0.210)6	0.168-0.202(0.185)6
Eastern(?) Nicaragua	...	0.237
Pacific slope of northwestern and central Costa Rica	0.189-0.225(0.208)6	0.158-0.209(0.187)4
Atlantic slope and southwestern Pacific slope of Costa Rica	0.230-0.309(0.275)4	0.274-0.294(0.284)2
Western Panamá	0.299	0.252-0.259(0.256)2
Central and eastern Panamá	0.272-0.306(0.292)9	0.245-0.270(0.259)7
Pacific coastal region of Colombia	...	0.245-0.266(0.256)2
Atlantic coastal region of Colombia	...	0.216-0.251(0.234)2
Cordillera Occidental of Colombia	0.247	...
Cordillera Central of Colombia	0.253-0.324(0.281)6	0.213-0.252(0.234)7
Cordillera Oriental of Colombia	0.269-0.337(0.301)3	0.252
Amazonian region of Colombia	0.202-0.257(0.238)3	0.195-0.220(0.208)2
Cordillera de Mérida de Venezuela	0.256	0.223-0.231(0.227)2
Caribbean coastal plain of Venezuela	0.265	0.216-0.233(0.226)4
Cordillera de la Costa of Venezuela	0.238-0.292(0.263)4	0.215-0.248(0.234)6
Guiana highlands of Venezuela	...	0.200-0.218(0.209)2
Trinidad	0.219-0.259(0.242)5	0.189-0.236(0.207)11
Tobago	0.222-0.275(0.256)3	0.241
Guyana	0.235-0.254(0.248)7	0.252
Surinam	0.246	...
Brazil	0.223-0.263(0.242)6	0.224-0.232(0.228)2
Argentina	0.259	0.231
Bolivia	0.240-0.257(0.246)5	0.200-0.218(0.209)2
Coastal plain of Ecuador	0.227-0.275(0.251)2	...
Western slopes of Andes in Ecuador	0.193-0.359(0.262)7	0.246-0.282(0.263)4
Inter-Andean basins of Ecuador (Pacific drainage)	...	0.223
Inter-Andean basins of Ecuador (Atlantic drainage)	0.273	0.232
Oriente of Ecuador	0.229-0.275(0.257)9	0.215-0.249(0.233)4
Andean Cordillera in Perú	0.228	...
East Andean slopes in Perú	0.190-0.247(0.224)8	0.186-0.274(0.218)7
Tropical lowlands of Perú	0.192-0.258(0.224)15	0.181-0.215(0.201)6

One specimen from Perú has the left upper postocular fused with the supraocular.

Temporals.—All specimens have 1+1 temporals, although many specimens (exact number not determined) have the posterior temporal divided vertically in two.

Relative tail length.—Relative tail length in the *Tantilla melanocephala* population system ranges from 0.180-0.359 in males and 0.158-0.294 in females (Table 6). The highest value in males is for a specimen from the western slopes of the Andes in Ecuador and for females a specimen from southwestern Costa Rica. The lowest count for males is for a specimen from western Nicaragua, and for females a specimen from western Nicaragua. The mean values do not show the same pattern, due primarily to the occurrence of some extreme values in populations otherwise characterized by less extreme values. The highest mean value for males is for specimens from the Cordillera Oriental in Colombia and for females for specimens from the Atlantic slope and southwestern Pacific slope of Costa Rica. The lowest mean values for males are for specimens from northwestern and central Costa Rica, and for females for specimens from southern Guatemala.

As may be seen from Table 6, where sample sizes are large enough, males have a greater

relative tail length than females, with one exception. The exception involves specimens from the western slopes of the Andes in Ecuador where the mean values are virtually identical. The average percentage value difference between males and females is 0.028.

Relative tail length values are lowest in western Central America from southern Guatemala to northwestern and central Costa Rica in both sexes. There is a sharp increase in specimens from the Atlantic slope of Nicaragua and Costa Rica, southwestern Costa Rica and all of Panamá. The mean values are: northern males, 0.209; southern males, 0.288; northern females, 0.187; southern females, 0.261. This trend of high relative tail length values continues, with some variation, into the Pacific coastal areas of Colombia, the Andes of Colombia, and the western slopes of the Ecuadoran Andes.

Values tend to be lower on the Amazonian side of South America than in the Andes and on the Pacific slopes. The mean values are, respectively: males, 0.242, 0.266; females, 0.219, 0.263. There is variation, however, in relative tail length values in Amazonian South America, with values being relatively high in Venezuela, the Guianas, Brazil, Argentina, and Amazonian Ecuador and relatively low in Bolivia and eastern Perú. Relative tail length values decrease in Trinidad, relative to those in Venezuela, but increase again in Tobago.

This pattern of variation follows, in broad outlines, that in subcaudal numbers.

In summary, as has been demonstrated with many wide-ranging species of Neotropical reptiles and amphibians, the patterns of variation of the various characteristics are discordant with respect to one another. It is for this reason and because we feel that recognition of infraspecific taxa does not adequately reflect the complexity of variation in biological species, that no subspecies are recognized.

Concordance in variation in color pattern and in ventrals and subcaudals in Central America, however, may lead some workers to adopt a somewhat different approach to interpretation of the above-discussed variational picture. As stated above, we consider specimens from Panamá to be intermediate between those making up pattern types A and B. The distinctions between specimens exhibiting patterns A and B, however, are made even more trenchant with consideration of ventral and subcaudal differences. Members of pattern A have 155-174 ($\bar{x}$ =165.0) ventrals in males and 158-177 ($\bar{x}$ =169.2) in females. Subcaudals vary from 46-59 ($\bar{x}$ =53.9) in males and from 42-60 ($\bar{x}$ =46.9) in females. Members of pattern B have 142-148 ($\bar{x}$ =144.2) ventrals in males and 143-155 ($\bar{x}$ =147.4) in females. Subcaudals vary from 64-82 ($\bar{x}$ =72.8) in males and from 63-75 ($\bar{x}$ =68.5) in females. There is no overlap between any of the ranges and the distinctions could easily point to the existence of 2 species. It is only with consideration of specimens from central and eastern Panamá that we are able to justify considering the specimens exhibiting patterns A and B as part of the *Tantilla melanocephala* population system and it is on this point that other workers might differ in their interpretation. As mentioned above, specimens from Panamá most closely resemble pattern A specimens in color pattern and pattern B specimens in ventral and subcaudal numbers. The color pattern situation has been summarized in Table 2 and demonstrates that the pattern of Panamanian specimens is intermediate between those of pattern A specimens and pattern B specimens, but is closer to that of pattern A specimens. Panamanian specimens have 139-149 ($\bar{x}$ =143.5) ventrals and 69-79 ($\bar{x}$ =75.1) subcaudals in males; corresponding ranges and means for females are 143-154 (152.0) and 66-71 (68.3). They most closely resemble, therefore, pattern B specimens and are not, for the most part, intermediate between the numbers exhibited by pattern A and B specimens. Some workers might prefer to recognize pattern A and B specimens as distinct from each other at the species level and each in turn distinct from the Panamanian specimens, which would then represent the population at the northern edge of the range of the South American species (comprised of our pattern types C-F). In that case, pattern A and B specimens would take the names *Tantilla armillata* Cope and *Tantilla ruficeps* (Cope), respectively. Our stand, of course, is based on the intermediacy of the pattern of the Panamanian specimens. Also, the closer resemblance of the pattern of the Panamanian specimens to that of pattern A specimens and the resemblance of ventral and subcaudal numbers to those of pattern B specimens lends further support to this argument.

The Status of the Names Associated with the *Tantilla melanocephala* Population System

Eleven names have been associated in various ways with the *Tantilla melanocephala* population

system in the past. These names are: (1) *Coluber melanocephalus* Linnaeus, 1758; (2) *Elapomorphus mexicanus* Günther, 1862; (3) *Tantilla armillatum* Cope, 1876*a;* (4) *Homalocranion melanocephalum* var. *fuscum* Bocourt, 1883; (5) *Tantilla pallida* Cope, 1887*b;* (6) *Pogonaspis ruficeps* Cope, 1894; (7) *Homalocranium melanocephalum* var. *fraseri* Günther, 1895; (8) *Homalocranium melanocephalum* var. *pernambucense* Günther, 1895; (9) *Homalocranium longifrontale* Boulenger, 1896*b;* (10) *Homalocranium hoffmanni* Werner, 1909; (11) *Elapomorphus nuchalis* Barbour, 1914. Another name, *Tantilla capistrata* Cope, 1876*b*, is associated with a taxon that has been recognized as a subspecies *(T. melanocephala capistrata)* by some workers but is herein raised to species level (see species accounts below). We have been able to examine the holotype or a portion of the syntype series upon which 5 of the above names are based. Types are lost or were not designated for 2 of the above-listed names. The holotype upon which one name is based was not available to us, but notes on it have been provided, and it was not necessary to examine 3 others.

The status of these 11 names is discussed below.

(1) *Coluber melanocephalus* Linnaeus, 1758 (type locality: "America"). This is the oldest name in the group and is the name we used for the above-described population system, in spite of the fact that no holotype was designated and there is no specific type locality. Andersson (1899), however, apparently identified the holotype of *Coluber melanocephalus* from among 2 specimens in the Royal Museum in Stockholm bearing that name. One of these 2 specimens is a *Sibynophis subpunctatus*, which is superficially similar to *Tantilla melanocephala*. The other specimen is a *T. melanocephala*, according to Andersson (1899). Unfortunately, Linnaeus (1758) described the *Tantilla* in the text, but figured the *Sibynophis*. Andersson (1899) chose to apply the name *Coluber melanocephalus* to the specimen described in the text, a decision with which we are in accordance. This specimen has 142 ventrals and 62 subcaudals and cannot be pinned down to locality on this basis, except to say that it came from South America.

(2) *Elapomorphus mexicanus* Günther, 1862 (type locality: "?Mexico"). This name is based upon the holotype (BMNH 1946.1.8.58), which purportedly came from "México." According to Hobart M. Smith (in litt.), no other specimens of this group have been forthcoming from México. The data accompanying the holotype, which we have examined, reads "?Mexico," although other authors (Günther, 1862, 1895; Smith, 1942; Stuart, 1963; Peters and Orejas-Miranda, 1970) have given the type locality as "Mexico," without the interrogative prefix. Smith (1942) stated "Boulenger (Cat. Snakes, vol. 3, 1896, p. 216) concludes that the type (labelled Salle's collection) was not collected by Salle and is not from Mexico. There are facts, however, which indicate that it may actually have come from Mexico. Although the ventral count is matched by some South American specimens, it is lower than any Central American specimen related to *T. melanocephala* (i.e., *T. armillata*). Another specimen from Dueñas, Guatemala, referred by Boulenger (Cat. Snakes, vol. 3, p. 221) to *T. fusca* and by Günther to *T. armillata* very closely matches the characters of *T. mexicana*, to which we have referred it. There is little doubt that these are distinct from *T. armillata*, and it is scarcely likely that they can be termed the same as the geographically distant *T. melanocephala*."

As mentioned above, we have examined the holotype of *Elapomorphus mexicanus* and, even though the specimen is faded, it is possible to determine its affinities clearly. In all features of color pattern, this specimen agrees with pattern F specimens from the western slopes of the Andes in Ecuador. Thus *Elapomorphus mexicanus* is technically a synonym of *Tantilla fraseri*, should the latter be resurrected in the future. No members of the *Tantilla melanocephala* group are known, therefore, from Mexico.

We have also examined the specimen (BMNH 75.5.1.2) from Dueñas, Guatemala, mentioned by Smith (1942) as very closely matching the characters of the holotype of *T. mexicana*, and find it does not resemble that specimen at all but rather is a typical member of the pattern A group of *Tantilla melanocephala (Tantilla armillata* auctorum).

(3) *Tantilla armillata* Cope, 1876*a* (type locality: "middle Costa Rica"). Cope (1876*a*) based this name on a single specimen (ANSP 3363), which now has the locality "San José" attached to it. This specimen is typical of pattern A specimens in all features. Pattern A specimens have been called *Tantilla armillata* by most previous workers (see synonymy of *T. melanocephala* below).

(4) *Homalocranion melanocephalum* var. *fuscum* Bocourt, 1883 (type locality: "Guatemala").

Stuart (1963) used the name *T. mexicana* hesitantly for material of the *T. melanocephala* group from Guatemala. Apparently, he had available 3 specimens (no more are now known). One was the Dueñas specimen mentioned above in the discussion of the name *Elapomorphus mexicanus*. A second was a specimen (UMMZ 106758) from Finca La Gloria, Depto. Santa Rosa, which also has the A pattern. The third specimen (MNHN 6059) is the holotype of *Homalocranion melanocephalum* var. *fuscum* Bocourt, 1883, purportedly from "Guatemala." This latter specimen did not come from Guatemala. Rather it resembles pattern E specimens from the Amazonian lowlands of Ecuador and Perú. Should a future worker desire to recognize pattern E specimens as a subspecies, the name *fusca* would then be available.

Boulengers's (1896*a*) usage of the name *fusca* also includes a peculiar *Tantilla jani*-like specimen from Nicaragua (Wilson and Meyer, 1971).

(5) *Tantilla pallida* Cope, 1887*b* (type locality: Chupada [=Chapada do Guimaraes, 56°15'W, 15°34'S] Est. Mato Grosso, Brazil). We have examined the holotype of *Tantilla pallida* (ANSP 11215) and find it a typical representative of pattern C type. The head is brown, the nuchal collar is divided medially, the dark nape band is dark brown and is followed by a pale neck band, the dorsum is tan and there is neither a middorsal dark stripe nor a pale lateral band. There are 148 ventrals and 58+ subcaudals (tip of tail missing). In these features it agrees with other specimens from Brazil. Should future workers wish to recognize the C-D pattern specimens as a distinct subspecies, the above name would be available.

The type locality of this specimen has been given simply as "Mato Grosso, Brazil" (Peters and Orejas-Miranda, 1970), but Malnate (1971) listed it as "Brazil, Matto Grosso, Chapada." Cope (1887*b*) indicated in his introduction that all the specimens mentioned in that paper came from or in the vicinity of Chupada [=Chapada], which is a small town located about 48 km northeast of Cuiaba in the state of Mato Grosso.

(6) *Pogonaspis ruficeps* Cope, 1894 (type locality: Jimenez, Costa Rica). Although we had previously considered the holotype of *Pogonaspis ruficeps* to have been in the collections of the museum of the Universidad de Costa Rica and not presently locatable Douglas C. Robinson recently informed us that he had located the type in the American Museum of Natural History. This male specimen (AMNH 17272), kindly supplied by Charles W. Myers, is in relatively poor condition and the pattern is somewhat faded but is clearly of the pattern B type. In addition, the ventrals number 144 (our count), which is a typical count for pattern B males.

(7) *Homalocranium melanocephalum* var. *fraseri* Günther, 1895 (type localities: Quito, Ecuador and "W. Ecuador"). We have examined 1 of 4 syntypes (BMNH 1946.1.9.84) upon which this name is based and find it to be in complete agreement with specimens exhibiting pattern F. This name is thus available for that population, should some future worker wish to use it.

(8) *Homalocranium melanocephalum* var. *pernambucense* Günther, 1895 (type locality: Pernambuco, Brazil). We have not examined the syntype series upon which this name is based and A.F. Stimson stated (in litt.) that the British Museum (Natural History) has only a single specimen from the original series and that the location of the remainder is not known. Günther's (1895) description indicated that the name applies to members with the type C pattern as he stated that there is no black dorsal stripe. The ventral counts of 149-154 given fit within the range for other Brazilian material, but the subcaudal counts of 30-32 are obviously for specimens with incomplete tails.

(9) *Homalocranium longifrontale* Boulenger, 1896*b* (type locality: Cali, Colombia). We have not examined the holotype (BMNH 1946.1.8.84), but A.F. Stimson has kindly sent us some detailed notes on pattern and scutellation. The color pattern description agrees with that of intergradient specimens from Panamá and Colombia.

(10) *Homalocranium hoffmanni* Werner, 1909 (type locality: "Guatemala"). We have been informed by Werner Ladiges (in litt.) of the Zoologisches Institut und Zoologisches Museum of the Universität Hamburg that the holotype of *Homalocranium hoffmanni* was destroyed during World War II. The description given by Werner (1909), however, is sufficiently detailed to indicate to us that the holotype did not come from Guatemala. Werner (1909) described the color pattern as follows (translation ours): "dorsum dark gray; a yellow middorsally broken neck band on the posterior half of the parietals and adjacent lateral scales. Venter whitish, only the throat gray (posterior chin shields whitish). Anal flecked with gray." There is no mention of a dark middorsal stripe and the pale nuchal collar is broken middorsally but not laterally. These 2 characters are not those of specimens from Guatemala (of the

pattern A type), which have 2 small nuchal spots confined to the parietals and a middorsal dark stripe. The above-cited characteristics are those of pattern C specimens, however. The ventral count of 155 (the tail is incomplete) does not allow us to narrow the type locality; all we can say is that the holotype of *Homalocranium hoffmanni* came from somewhere in eastern South America.

(11) *Elapomorphus nuchalis* Barbour, 1914 (type locality: Villa Bella on the Amazon River, above Santarém, Brazil). We have not examined the holotype (MCZ 1164) upon which this name is based, but Barbour's (1914) description is sufficiently detailed to indicate to us that the specimen exhibits a pattern intermediate between that of C and D. He mentioned that there are "three very indistinct darker longitudinal lines which are just visible on the nape region which disappear along the body and reappear upon the posterior extremity of the body and on the tail." Also, he pointed out that the nuchal collar is divided medially only. The ventral count of 147 (the tail is incomplete) falls within the range for other Brazilian material.

Species Accounts

Tantilla **andinista**, sp. nov.

Holotype.—KU 135209.

Type locality.—5 km E Alausí, Prov. Chimborazo, Ecuador, elevation 2600-2750 m, collected 9 June 1970 by T.H. Fritts.

Diagnosis.—A member of the *Tantilla melanocephala* group with a pattern consisting of a large amount of pale markings on the head on a dark brown background, a tan dorsal ground color, a narrow dark middorsal stripe (confined to middle of the middorsal row), and a narrow pale lateral stripe (confined to the upper half of row 3). The head pattern consists of an extensive pale marking on the snout, continuing posteriorly over the supraocular and anterolateral corner of the parietal downward onto the postoculars, anterior portion of the anterior temporal and supralabials 4, 5, and 6. The dark head cap is followed by a wide middorsally divided pale nuchal band, then a dark nape band, and finally by a pale neck band (Figs. 7, 12A).

Description of the holotype.—An adult female with 15 dorsal scale rows, smooth throughout, 157 ventrals, divided anal plate, 50 subcaudals, total length 285 mm, tail length 56 mm, relative tail length 19.6%.

Nasal scale completely divided, the posterior section separated from the single preocular on both sides of the head; 2 postoculars, subequal in size; one anterior temporal, posterior temporal divided into 2 small scales, approximately the size of a dorsal scale; supralabials 7-7, with the 3rd and 4th entering the orbit, last one largest; infralabials 6-7, four in contact with the anterior chin shields on left and 5 on right, 4th largest on left and 5th on right, first pair in broad medial contact; anterior chin shields larger than posterior pair.

The middorsal stripe is dark brown, narrow, and confined to the middle of the middorsal scale row. Anteriorly this stripe contacts the dark nape band and continues to the end of the tail. The dorsal ground color is tan (pale brown in life, according to collector's field notes). The pale lateral stripe is confined to the upper half of row 3 and is bounded below by brown pigment on the lower half of row 3 and the upper edge of row 2. There is a brown spot at the end of each of the scales in row 1. The venter is immaculate cream (white with greenish tint in life).

The head is dark brown above (black in life) with cream-colored markings. Most of the snout to the level of the posterior quarter of the prefrontals is cream, except for dark brown pigment on the lower half of the rostral and around the anterior end of the naris. The pale snout is connected to a pale spot on the supraocular, which is, in turn, connected (but not on left) to a pale spot on the anterolateral corner of the parietal. This latter spot is in contact with the postocular pale spot occupying both postoculars, the anterior one-third of the anterior temporal, the posterior half of supralabial 4, all of 5,and the anterior half of 6. A dark subocular spot is present on the posterior half of supralabial 2, all of 3, and the anterior half of 4. The dark head cap is bounded posteriorly by a cream-colored nuchal band beginning on the posterior portion of the parietals and extending about one dorsal scale posterior to the parietals. This pale nuchal band is completely divided medially by a connection about one dorsal scale wide between the head cap and the dark nape band. The dark nape band is three dorsal scales long and is followed by a well-defined cream-colored neck band about one dorsal scale in length. There is a dark blotch on the mental and a circular dark blotch on the anterior portion of supralabial 4 (5 on right).

Range.—Known only from the type locality in the Alausí Basin of Ecuador (Fig. 13).

Etymology.—The name *andinista* is from the Spanish, meaning "wanderer among the Andes"

in allusion to the montane distribution of this species.

Habitat notes.—The holotpe was found under a rock during the day.

Tantilla capistrata Cope

Tantilla capistrata Cope, 1876*b:* 181.

Homalocranium melanocephalum: Boulenger, 1896*a:* 215 (part).

Tantilla melanocephala: Dunn, 1923: 186; Parker, 1938: 445.

Tantilla melanocephala capistrata: Schmidt and Walker, 1943*b*: 318; Peters, 1960: 539; Peters and Orejas-Miranda, 1970: 295.

Holotype.—ANSP 11581.

Type locality.—Valley of Jequetepeque, Depto. La Libertad, Perú.

Diagnosis.—A member of the *Tantilla melanocephala* group with a head pattern consisting of a pale brown to dark brown head cap separated from a dark brown nape band by a well-defined complete or medially divided pale nuchal band. There is an extensive pale marking on the snout covering all the internasals and the anterior one-half to three-quarters of the prefrontals. The dorsal pattern consists of a narrow, diffuse dark brown middorsal stripe confined to the middorsal scale row (if present) on a tan ground color. There is no pale lateral stripe (Figs. 8, 12B).

Description.—*Tantilla capistrata* has a tan dorsum without a dark middorsal stripe or only a slight indication of one. There is no pale lateral band. The venter is immaculate cream.

The head is dark brown (juveniles) to brown or pale brown (adults) above. The snout is pale cream up to the level of the posterior one-fourth to two-thirds of the prefrontals. A pale to dark brown head cap follows and covers the top of the head except for the posterior tips of the parietals. The preocular pale spot is in contact with the pale snout markings dorsally and with the postocular pale spot posteriorly underneath the subocular dark spot, which does not reach the lip. The postocular pale spot is separated from the pale nuchal band by an extension of the dark head cap.

The pale cream nuchal band is complete (4 specimens) or divided medially (4 specimens) and is bounded posteriorly by a dark brown nape band 2½–5 dorsal scales long. This band is in turn bounded posteriorly by a pale neck band (absent in one specimen) 1–1⅓ dorsal scales long. There is very little dark pigment on the infralabials, consisting of dark smudges on some of the first 4 infralabials, if present.

Variation in scutellation may be summarized as follows: prefrontals in contact with second supralabial on both sides in all specimens; first pair of infralabials usually in contact medially (87.5%), but may be separated (12.5%); ventrals in males 130-150 ($\bar{x}$ =142.0), in females 135-156 ($\bar{x}$ =147.5); subcaudals in males 53-61 ($\bar{x}$ =57.0), in females 46-71 ($\bar{x}$ =56.3).

Total length in snakes of all ages ranges from 134-360 mm (one specimen measures 394 mm overall with an incomplete tail; judged by relative tail length of other females, this snake may have had a total length of 428-462 mm), and tail length ranges from 31-87 mm (the large specimen mentioned above may have had a tail length of from 84-119 mm). Relative tail length ranges from 19.5-25.4%.

Geographic variation.—The range of *Tantilla capistrata* is broken into 2 disjunct sections, one in the northwestern portion of coastal Perú and the other in the semiarid valleys of the Marañon, Chinchipe, and Chamaya rivers. Although the basic details of pattern are similar, there are differences between the two geographic groupings, nonetheless. All specimens from the valley of the upper Marañon (Atlantic drainage—hereinafter referred to as the eastern segment) have no evidence of a dark middorsal stripe. All specimens from northwestern coastal Perú (Pacific drainage—hereinafter referred to as the western segment) have a dark middorsal stripe, although it is very narrow and diffuse (even reduced to one spot per scale), except one (ANSP 11581, the holotype). The dark nape band of members of the eastern segment ranges from 2½-4 scales long ($\bar{x}$ =3.0), that of members of the western segment 3-5 ($\bar{x}$ =3.7). Both ventral and subcaudal numbers are higher in the eastern segment, except for subcaudals of females (Table 7). The mean for subcaudals of females from the western segment is as high as it is because the subcaudal count of the holotype (ANSP 11581) is 71. This is the highest count for the species (males included—the highest male count is 61). The ventral count of 156 is also the highest for the species. Thus the total of ventrals and subcaudals for the holotype is also the highest for the species (227, as opposed to a high count of 210 for males and 190 for other females). The holotype is also the only specimen from the western segment without a vestige of a middorsal stripe. The reason for the differences between the holotype and other specimens of the species remains unexplained and will until additional material from

Table 7. Comparison of ventral and subcaudal numbers in the eastern and western segments of the range of *Tantilla capistrata*.

Character	Eastern segment	Western segment
Ventrals		
♂♂	147-150(148.5)2	130-141(135.5)2
♀♀	155	135-156(145.0)3
Subcaudals		
♂♂	60-61(60.5)2	53-54(53.5)2
♀♀	...	46-71(56.3)3

critical areas accumulates.

Range.—From near sea level to moderate elevations of northwestern coastal Perú and the valleys of the upper Río Marañon, Río Chinchipe, and Río Chamaya (Fig. 14).

Ecological distribution.—No direct information on ecological distribution is available but judged by the available locality records, *Tantilla capistrata* occurs in at least 2 apparently disjunct populations, one occupying the arid coastal desert regions of northwestern Perú and the other the semiarid inter-Andean basin formed by the valleys of the upper Río Marañon, Río Chinchipe and Río Chamaya. According to Dixon and Wright (1975), the "xerophyllous vegetation of these valleys is not continuous with that of the coastal area."

Locality records.—Perú: Depto. Cajamarca, 3 km NE Chamaya (LSUMZ 19557); 5 km S Jaén, 900 m (LSUMZ 19558); Perico (MCZ 17391); Depto. La Libertad, Chiclin (FMNH 33749, 34286-87); valley of [Río] Jequetepeque (ANSP 11581); Depto. Piura, Sullana (NMB 15631).

Tantilla **equatoriana**, sp. nov.

Holotype.—USNM 198530.

Type locality.—San Lorenzo, Prov. Esmeraldas, Ecuador, collected in May 1951 by M. Olalla.

Diagnosis.—A member of the *Tantilla melanocephala* group with a head pattern consisting of a dark head cap grading into a dark nape band and punctuated by pale spots located near the posterior end of the parietals (and extending onto the posterior temporal and 1 or 2 adjacent postparietal scales), a preocular pale spot that continues posterodorsally onto the preocular scale to touch the eye, and a postocular spot that is in contact with pale pigment on the lateral gulars (opposite the parietal spots), not separated by a dark lateral extension of the head cap. No pale neck band is present posterior to the dark nape band. The dorsal pattern is bold with dark brown stripes on a tan ground color located on the middle of row 1, from the upper half of row 2 to the lower half of row 3, upper edge of row 4 to lower middle portion of row 5, middle of row 6 and the middle of the middorsal scale row. The subcaudals are relatively high, ranging from 77 to 79 (Figs. 9, 12C).

Description of holotype.—An adult (?) male with 15 dorsal scale rows, smooth throughout, 147 ventrals, divided anal plate, 79 subcaudals, total length 253 mm, tail length 72 mm, relative tail length 28.5%.

Nasal scale completely divided, the posterior section separated from the single postocular on both sides of the head; two postoculars, subequal in size; one anterior and one posterior temporal, both elongate; supralabials 7-7, with the 3rd and 4th entering the orbit, last one largest; infralabials 6-6, four in contact with the anterior chin shields, 4th largest, first pair in broad medial contact; anterior chin shields larger than posterior pair.

The middorsal stripe is dark brown, well-defined, covering the middle of the middorsal scale row and expanding at intervals to cover the medial apices of the scales of the paravertebral row. Anteriorly this stripe contacts the dark nape band and continues to the end of the tail. The dorsal ground color is tan. The lateral stripe pattern consists of: a narrow dark brown stripe on the middle of row 1; a dark brown stripe extending from the upper half of row 2 to the lower half of row 3; a pale cream-colored stripe from the upper half of row 3 through most of row 4; a narrow, diffuse dark brown stripe from the upper edge of row 4 through the middle of row 5; a narrow dark brown stripe through the middle of row 6. The venter is immaculate cream.

The head is brown above with pale markings on the upper portion of the rostral and anterior half of the internasals and a pair of pale spots located

on the posterior portion of the parietals and a portion of the adjacent posterior temporal and 2 postparietal scales. The pale preocular spot occupies most of supralabials 1 and 2 and extends posterodorsally onto the preocular and touches the eye. The preocular and postocular pale spots are separated by a dark subocular blotch occupying most of supralabials 3 and 4 (and a thin strip along the posterior edge of supralabial 2), except for the anteroventral corner of each. This dark pigment is also present along the lower edge of supralabials 5 through 7. The postocular pale spot is present on the lower portion of the anterior temporal and the upper portion of supralabials 5 through 7 (separated from the brown head cap by a dark brown stripe coursing through the middle of the anterior temporal and onto the dorsal portion of the 7th supralabial) and is in contact with the pale pigment on the lateral gulars (opposite the parietal spots) and is not separated by a lateral extension of the dark head cap.

The dark head cap grades into a dark brown nape band which extends posteriorly to the fourth dorsal scale posterior to the parietals. There is no pale band posterior to the dark nape band. The mental is largely dark brown and there is a dark brown blotch along the posterior suture of each infralabial.

Paratype.—USNM 198429, same locality as holotype.

Variation in the paratype.—The dorsal pattern of the male paratype is essentially like that of the holotype. The only pattern differences are minor; the dorsum of the head is dark brown and the pale parietal spots are slightly elongated anteriorly.

Scutellation is the same for the paratype as for the holotype, except that the paratype has 142 ventrals and 77 subcaudals. Total length is 218 mm, tail length 59 mm, and the relative tail length is 27.1%.

Range.—Known only from the type locality (Fig. 13).

Etymology.—The name *equatoriana* is from the Latin meaning "equator," referring to its distribution and its country of origin.

Ecological distribution.—Lowland rain forests of northwestern coastal Ecuador.

Tantilla **insulamontana**, sp. nov.

Holotype.—KU 152207.

Type locality.—Río Minas, 15.1 km W Santa Isabel, Prov. Azuay, Ecuador, elevation ≈ 1250 m, collected 12 June 1971 by A.C. Echternacht.

Diagnosis.—A member of the *Tantilla melanocephala* group with a head pattern consisting of a brown head cap with 2 horn-shaped anterior extensions, nuchal spots confluent with dorsal ground color, and no dark nape band. The dorsal pattern consists of numerous dark stripes on a more-or-less uniform tan ground color. There are diffuse stripes through the middle of scale row 1, on the upper half of row 2 and lower half of row 3, through the middle of row 4, on the upper half of row 5 and the lower half of row 6. A relatively dark, well-defined stripe courses down the middle of the middorsal row and is connected to dark markings along the medial edges of the scales of the paravertebral rows, giving the whole stripe a hatched appearance (Figs. 10, 12D).

Description of holotype.—An adult (?) male with 15 dorsal scale rows, smooth throughout, 144 ventrals, divided anal plate, 65 subcaudals, total length 249 mm, tail length 67 mm, relative tail length 26.9%.

Nasal scale completely divided, the posterior section separated from the single postocular on both sides of the head; 2 postoculars, subequal in size; one anterior and one posterior temporal, both elongate; supralabials 7-7, with the 3rd and 4th entering the orbit, last one largest; infralabials 6-6, four in contact with the anterior chin shields, 4th largest, first pair broadly separated by contact of mental and anterior chin shields; anterior chin shields larger than posterior pair.

The middorsal stripe is dark brown, occupies the middle of the middorsal scale row and is connected to dark markings along the medial edges of the scales of the paravertebral rows. Anteriorly this stripe contacts the dark head cap at the posterior end of the medial parietal suture and continues onto the end of the tail. The dorsal ground color is tan. The lateral stripe pattern consists of: a diffuse brown stripe through the middle of scale row 1 accentuated by a dark brown spot at the posterior end of each scale; a diffuse brown stripe on the upper half of row 2 and the lower half of row 2 with a dark dot at the posterior end of the scales of each of those 2 rows; a broad, diffuse brown stripe through the middle of row 4, each scale of which is rimmed anteriorly by darker pigment; a diffuse brown stripe on the upper half of row 5 and the lower half of row 6, each scale of both rows outlined anteriorly by dark pigment. The venter is cream with a single brown spot at the lateral edges of each ventral.

The head is brown above. From the anterior edge of the head cap extend 2 horn-shaped or

comma-shaped dark brown marks onto the middle of the internasals. They border a posteromedial extension of the pale pigment on the snout that extends back to the juncture between the prefrontals and frontal. A pair of pale parietal spots are present on the posterior portions of the parietals and are confluent with the dorsal ground color on either side of the middorsal stripe. There is no dark nape band. The pale preocular spot on supralabials 2 and 3 is confluent with the pale pigment on the snout and also with the pale postocular spot on the posterior portion of supralabial 4, all of 5, most of supralabial 6, the lower portion of the upper postocular, all of the lower postocular, and the anterior third of the anterior temporal. The subocular dark spot is limited to a narrow rim of dark pigment around the bottom of the eye. A lateral dark extension of the head cap on the posterior edge of supralabial 6 and the anterodorsal two-thirds of supralabial 7 completely separates the postocular pale spot from the pale pigment of the lateral gulars opposite the parietal spots.

There are spots of brown pigment on the mental, all infralabials except the last, and the anterior chin shields.

Paratypes.—Three, all from Prov. Azuay, Ecuador: Llunguilla [=Yunguilla] (CAS 94090-91) [not mapped]; 10 km SW Girón, 2100 m (USNM 198430).

Variation in the paratypes.—The dorsal pattern of all paratypes, which are all females, is essentially the same as that of the holotype, even granting that one specimen is slightly faded (CAS 94091) and another was preserved just prior to shedding (USNM 198430). One specimen (CAS 94090) shows evidence of a complete pale nuchal collar extending posteroventrally from the parietals. It terminates at the dark stripe on rows 2 and 3.

Variation in scutellation in the female paratypes may be summarized as follows: ventrals 152-157 ($\bar{x}$=154.3)-3 specimens; subcaudals 59-61 ($\bar{x}$=60.0)-2 specimens. All other aspects of scutellation agree with that of the holotype. Total length of snakes of all ages ranges from 310-404 mm, and tail length ranges from 70-95 mm. Relative tail length ranges from 22.5-23.5%.

Range.—Intermediate elevations of the Hoya de Jubones (Pacific drainage) in southern Ecuador (Fig. 13).

Etymology.—The name *insulamontana* is from the Latin, meaning "island in the mountains," referring to the distribution of this species in an isolated intermontane basin.

Habitat notes.—The holotype was collected as it moved along an embankment adjacent to a road beside a bamboo thicket along a river at 13:30 hours on an overcast day.

Tantilla **lempira**, sp. nov.

Holotype.—LSUMZ 26093.

Type locality.—41 km NW Tegucigalpa, Depto. Francisco Morazán, Honduras, collected 3 June 1968 by Ernest A. Liner.

Diagnosis.—A member of the *Tantilla melanocephala* group with a head pattern consisting of a brown head cap with a pair of small, indistinct nuchal spots largely confined to the scales posterior to the parietals. There is no dark lateral extension of the head cap between the postocular pale spot and the pale pigment on the lateral gulars. The dorsal ground color is pale brownish-gray and there is a dark ventral border below the pale lateral stripe. The prefrontal and second supralabial are separated from one another by contact of the postnasal and preocular. The ventrals and subcaudals are relatively low (Figs. 11, 12E).

Description of holotype.—An adult ♀ with 15 dorsal scale rows, smooth throughout, 153 ventrals, divided anal plate, 36 subcaudals, total length 258 mm, tail length 40 mm, relative tail length 15.5%

Nasal scale completely divided, the posterior section in contact with the single preocular on both sides of the head; 2 postoculars, subequal in size; one anterior and one posterior temporal (posterior temporal on right divided vertically into 2 scales), both elongate; supralabials 7-7, with the 3rd and 4th entering the orbit, last one largest; infralabials 6-6, four in contact with the anterior chin shields, 4th largest, first pair in narrow medial contact; anterior chin shields larger than posterior pair.

The middorsal stripe is dark brown, narrow, disjunct, composed of a series of dots, one each at the posterior end of each scale of the middorsal row. Anteriorly this stripe contacts the dark nape band and fades out just posterior to the vent. The dorsal ground color is pale brownish-gray. The pale lateral stripe is present on the upper half of row 3 and the lower half of row 4 and is barely discernible. The pale lateral stripe is bounded below by a dark line on the lower half of row 3. The venter is immaculate cream.

The head is brown above. A barely visible pale spot is present on the upper portion of the rostral

and medial portions of the internasals. The pale nuchal spot on the right side of the head (none is visible on the left) is small and barely discernible and is confined to the point near the juncture of the parietal, posterior temporal, and adjacent postparietal scales. The preocular pale spot is present on supralabials 1 and 2 and is separated from the postocular pale spot by a subocular dark spot on supralabials 3 and 4. The postocular pale spot is in contact with the pale pigment on the lateral gulars (opposite the pale nuchal spots), not separated by a dark lateral extension of the dark head cap. The dark head cap grades into the dark brown nape band, which extends 4 scales posterior to the parietals and is bounded posteriorly by a pale neck band. This pale neck band is one and one-quarter scales long and is divided middorsally by the dark middorsal stripe.

Paratypes.—Two, both from Honduras: 41 km NW Tegucigalpa, Depto. Francisco Morazán (LSUMZ 33737); Montserrat, Depto. El Paraiso (MCZ 49961).

Variation in the paratypes.—The dorsal pattern of both paratypes is essentially like that of the holotype. The middorsal dark stripes of both paratypes are better defined than that of the holotype. The dark nape band extends 3 scales posterior to the parietals in both specimens.

Variation in scutellation in the paratypes, both females, may be summarized as follows: ventrals 148-150 ($\bar{x}$ =149.0); subcaudals 36-44 ($\bar{x}$ =40.0). All other aspects of scutellation agree with that of the holotype. Total length ranges from 206-254 mm, and tail length ranges from 38-43 mm. Relative tail length ranges from 16.9-18.4%.

Range.—Moderate elevations of the Pacific versant of Honduras (Fig. 15).

Etymology.—The name *lempira* is that of an Indian chief who fought against the Spanish invasion of Honduras. It is also the name of a department in Honduras and of the Honduran monetary unit.

Ecological distribution.—All specimens came from within the Subtropical Moist Forest formation (*Pinus oocarpa* forest).

Tantilla melanocephala (Linnaeus)

Coluber melanocephalus Linnaeus, 1758: 218, 1766: 378; Gmelin, 1789: 1095; Shaw, 1802: 490; Daudin, 1803: 367.

Natrix melanocephalus: Merrem, 1820: 110.

Elaps melanocephalus: Wagler, 1824: 8.

Duberria melanocephala: Fitzinger, 1826: 55.

Lycodon melanocephalum: Boie, 1827: 526.

Cloelia melanocephala: Wagler, 1830: 187; Fitzinger, 1843: 23.

Calamaria melanocephala: Schlegel, 1837: 38.

Homalocranion melanocephalum: Duméril, Bibron and Duméril, 1854: 855; Jan and Sordelli, 1866: livr. 15; Bocourt, 1883: 588.

Tantilla melanocephala: Cope, 1861: 74, 1866: 126, 1868: 102, 1871: 205, 1876*a*: 142, 1876*b*: 181, 1887*a*: 83, 1900: 1111; Stejneger, 1902: 157; Griffen, 1916: 209; Ruthven, 1922: 68; Dunn, 1923: 186; Amaral, 1929*a*: 107, 1929*b*: 46, 1929*c*: 221, 1931; 93; Dunn and Bailey, 1939: 19; Smith, 1941: 115; Schmidt and Walker, 1943*a*: 293; Beebe, 1946: 43; Hoge, 1952: 221; Brongersma, 1956: 184; Roze, 1966: 224.

Elapomorphus mexicanus Günther, 1862: 57 (holotype, BMNH 1946.1.8.58; type locality: "?Mexico," in error).

Tantilla armillata Cope, 1876*a*: 143 (holotype, ANSP 3363; type locality: "middle Costa Rica"), 1887*a*, 1900: 1111; Dunn and Bailey, 1939: 19; Taylor, 1951: 152, 1954: 763; Mertens, 1952*a*: 74, 1952*b*: 93; Rand, 1957: 531; Smith, 1958: 224; Smith and Grant, 1958: 212; Hardy and Cole, 1967: 194; Myers and Rand, 1969: 4; Clark, 1970: 130; Peters and Orejas-Miranda, 1970: 294.

Homalocranium melanocephalum var. *fuscum* Bocourt, 1883: 589 (holotype, MNHN 6059; type locality: "Guatemala," in error).

Tantilla pallida Cope, 1887*b*: 56 (holotype, ANSP 11215; type locality: Chupada [=Chapada dos Guimaraes], Est. Mato Grosso, Brazil), 1900: 1111.

Pogonaspis ruficeps Cope, 1894: 204 (holotype, AMNH 17272; type locality: Jiménez, Costa Rica).

Homalocranium armillatum: Günther, 1895: 149.

Homalocranium melanocephalum var. *fraseri* Günther, 1895: 148 (syntypes, BMNH 1946.1.9.43-44 and BMNH 1946.1.8.77, 1946.1.8.80, 1946.1.9.84; type locality of first 2 specimens: Quito, Ecuador; of remaining 3: "W. Ecuador").

Homalocranium melanocephalum [var. *melanocephalum]:* Günther, 1895: 147.

Homalocranium melanocephalum var. *pernambucense* Günther, 1895: 148 (single available syntype, BMNH 80.11.25.5, location of remaining syntypes unknown *fide* A.F. Stimson; type locality: Pernambuco, Brazil).

Homalocranium mexicanum: Günther, 1895: 153.

Homalocranium melanocephalum: Boulenger, 1896*a*: 215; Andersson, 1899: 10; Schmidt and Inger, 1951: 463.

Homalocranium fuscum: Boulenger, 1896*a*: 220 (part).

Homalocranium longifrontale Boulenger, 1896*b*: 17 (holotype, BMNH 1946.1.8.84; type locality: Cali, Colombia), 1896*a*: 218.

Homalocranium ruficeps: Boulenger, 1896*a*: 223.

Homalocranium hoffmanni: Werner, 1909: 239 (number of holotype unknown; type locality: "Guatemala," in error); Amaral, 1929*b*: 46.

Elapomorphus nuchalis Barbour, 1914: 199 (holotype, MCZ 1164; type locality: Villa Bella, on the Amazon River above Santarem, Brazil); Amaral, 1929*b*: 46.

Tantilla longifrontale: Ruthven, 1922: 68; Dunn, 1944: 29; Beebe, 1946: 42.

Tantilla longifrontalis: Amaral, 1929*c*: 220, 1931: 93; Dunn, 1944: 208; Peters, 1960: 539; Roze, 1966: 222; Peters and Orejas-Miranda, 1970: 295.

Tantilla fusca: Amaral, 1929*c*: 220 (part).

Tantilla ruficeps: Amaral, 1929*c*: 221; Taylor, 1951: 156; Smith, 1958: 224; Smith and Grant, 1958: 212; Peters and Orejas-Miranda, 1970: 296.

Tantilla melanocephalus: Shreve, 1947*a*: 315, 1947*b*: 533.

Tantilla mexicana: Smith, 1942: 37; Hartweg, 1944: 4; Smith and Taylor, 1945: 139; Stuart, 1963: 118; Peters and Orejas-Miranda, 1970: 296.

Tantilla melanocephalum: Wehekind, 1955: 12.

Tantilla fraseri: Peters, 1960: 539; Peters and Orejas-Miranda, 1970: 294.

Tantilla melanocephala melanocephala: Peters, 1960: 539; Underwood, 1962: 169; Verteuil, 1968: 103; Peters and Orejas-Miranda, 1970: 295; Mertens, 1972: 16; Cordeiro and Hoge, 1973: 283; Achaval and Vaz-Ferreira, 1974: 107; Dixon and Soini, 1975: 5, 1977: 72.

Holotype.—Not designed; stated by Andersson (1899) to be in the Royal Museum in Stockholm.

Type locality.—"America."

Diagnosis.—A member of the *melanocephala* group with a variable color pattern that may be divided into 6 discrete types (see section on the *T. melanocephala* population system above). All populations of *Tantilla melanocephala* differ from *T. andinista* in not having the extreme amount of pale markings on the head of the latter, but rather having the pale markings restricted to the snout and nuchal collar. All populations of *T. melanocephala*, except for those containing pattern C specimens, differ from *T. capistrata* in having the nuchal collar divided medially and laterally, sometimes reduced to 2 parietal spots and a dark middorsal stripe present. Pattern C specimens differ from *T. capistrata* in usually (75.6% of specimens) having the nuchal collar divided both medially and laterally, whereas in *T. capistrata* the nuchal collar is always divided medially only or complete. In addition, smaller specimens of *T. capistrata* have a virtually black head and dark nape band, separated distinctly from the cream-collared snout markings and nuchal collar. *Tantilla equatoriana* differs from all *T. melanocephala* in having the pale preocular spot entering the orbit and in details of pattern (especially the presence of a dark stripe on dorsal scale row 6). The subcaudal counts of *T. equatoriana* are also higher than those of any *T. melanocephala* except for pattern B specimens and the intergradient specimens from Panamá and Colombia. All *T. melanocephala* differ from *T. insulamontana* in having the pale nuchal collar or spots not confluent with the dorsal ground color, but rather separated by a dark nape band, and in having no dark stripe located on the adjacent halves of dorsal scale rows 5 and 6. *Tantilla insulamontana* appears to the eye to be a *Tantilla* with a multilineate dorsal pattern on a pale background, without a dark nape band and with the pale nuchal spots confluent with the dorsal ground color, a pattern very different from that of any *T. melanocephala*. *Tantilla lempira* differs from *T. melanocephala* in having the pale nuchal spots largely confined to scales posterior to the parietals. It differs from most *T. melanocephala* (except pattern B specimens and occasional specimens in other pattern groups) in not having a dark lateral extension of the head cap separating the postocular pale spot and the pale pigment on the lateral gulars (opposite the pale nuchal spots). From pattern A specimens, the range of which is virtually parapatric with that of *T. lempira*, *T. lempira* differs in the following suite of characters (characters of *T. lempira* indicated in parentheses): nuchal spots distinct and occurring usually only on the parietals (nuchal spots indistinct and largely confined to scales posterior to the parietals); dorsal ground color tan to brown (pale brownish-gray); dark ventral border of pale lateral stripe not present (present); dark lateral

extension of head cap separating postocular pale spot and pale pigment on lateral gulars (opposite pale nuchal spots) present (absent); preocular and postnasal in contact separating the prefrontal and second supralabial (not in contact); ventrals 158-177 in females (148-153); subcaudals 42-60 in females (36-44) (Figs. 1-6).

Description.—*Tantilla melanocephala* is a widely-distributed snake and, as such, shows a wide range of variation in pattern and scutellational characteristics. What follows is a summarization of those characteristics: (1) head cap cream to dark brown, usually pale brown to dark brown; (2) pale nuchal collar complete, divided medially, divided medially and laterally or reduced to two small spots centered on the parietals (usually not complete); (3) dorsal ground color tan to brown; (4) dark subocular blotch completely separating pre- and postocular pale spots or not; (5) lateral extension of dark head cap present or not; (6) brown to dark brown dark nape band present or not; (7) pale neck band following dark nape band present or not, if present, occupying ½-2 dorsal scale lengths, sometimes reduced to small spots on either side of the dark middorsal stripe; (8) pale lateral band present or not, if present, usually occupying from as little as the upper portion of row 3 to as much as the upper portion of row 3, all of row 4, and the lower portion of row 5, bounded above and/or below with dark pigment or not.

Variation in scutellation may be summarized as follows: prefrontal in contact with second supralabial on one or both sides or not (in contact on both sides in 66.2% of specimens); first pair of infralabials in contact medially or not (in contact in 80.7% of specimens); ventrals in males 125-174, in females 134-177; subcaudals in males 41-92, in females 41-75.

Total length in snakes of all ages ranges from 95-486 mm and tail length ranges from 15-140 mm. Relative tail length ranges from 15.8-35.9%.

Range.—From near sea level to intermediate elevations along both versants from Guatemala throughout the length of Central America into South America as far south as southern Perú, Bolivia, northern Argentina, and Uruguay; also on the islands of Trinidad and Tobago (Figs. 14, 15).

Ecological distribution.—See section on distributional patterns.

Locality records.—We have arranged the specimens examined according to the pattern types discussed above.

Pattern A.—GUATEMALA: Depto. Sacatepequez: Dueñas (BMNH 75.5.1.2); Depto. Santa Rosa: Finca La Gloria (UMMZ 106758). EL SALVADOR: Depto. San Salvador: San Salvador (FMNH 64964). HONDURAS: Depto. Francisco Morazán: El Zamorano (AMNH 70180, 70195; MCZ 48701-02, 49882-85, 49920-21); 11 km N Sabana Grande (LSUMZ 26092); Tegucigalpa (BYU 18262); Depto. Olancho: Pataste (MSU 4724); Depto. Valle: San Lorenzo (AMNH 70228). NICARAGUA: Depto. Chontales: Juigalpa (KU 174315); Depto. Managua: Managua (UMMZ 89478); Las Robles (KU 174314); Depto. Matagalpa: 2 mi N Matagalpa (UMMZ 116517); 0.5 mi W Matagalpa (UMMZ 116515—2 specimens); 1 mi W Matagalpa (UMMZ 116514); 1.5 mi W Matagalpa (UMMZ 116516—2 specimens); Depto. Rivas: 12 km N Costa Rican border between Pan American Hwy. and Lake Nicaragua (KU 140077); Finca Amayo, 13 km S, 14 km E Rivas (KU 101922); within 3 km Moyogalpa, Isla de Ometepe (KU 86258). COSTA RICA: Prov. Guanacaste: 0.5 mi N Colonia Carmona (CRE 8221); 6 km NW Las Cañas (CRE 2905); Finca Taboga, ≈ 20 km SE Las Cañas (KU 102528-29; LACM 64595); 1 mi N, 2 mi E Santa Rosa (TCWC 17169); 1 km W Tilarán (UCR 1927); 4 km E Los Angeles de Tilarán (KU 35516-17); 0.1 mi SE Finca Jimenez (CRE 3087); 8.4 mi from Tilarán to Las Cañas (CRE 6280); Prov. Heredia: La Ribera, Belén (UCR 1038); Prov. San José: San José (ANSP 3363).

Pattern B.—NICARAGUA: no other data (USNM 15205). COSTA RICA: Prov. Cartago: 1 mi E Puente Río Reventazón (UCR 2144); Prov. Limón: Río Jimenez, Pococí (UCR 3370); Prov. Puntarenas: Finca Las Cruces, 6 km N San Vito de Java (RWM 6756); [Rincon, Peninsula de] Osa, near airport (LACM 125563); 4 km S San Vito (LACM 125562); Prov. San José, 10 mi NW San Isidro El General (KU 31960). PANAMÁ: Prov. Chiriquí: Finca Palosanto, ≈ 6 km WNW El Volcán (KU75758); Prov. Coclé: El Valle de Anton (KU 112495).

Intermediate specimens.—PANAMÁ: Prov. Darién: 0.5 mi S Camp Chucunaque (FMNH 170141); Prov. Panamá: Río Chagres (MCZ 37152); Río Chagres, Camp San Juan de Pequeni (MCZ 38243); Agua Clara, Chagres (ANSP 22267); Arraiján, Chorrera (ANSP 22277); El Aquacate, N of Capirá (UF/FSM 29869-70); La Cumbres (KU 75757); Isla Taboga (MCZ 9999); Panamá (MCZ 28048, 37114); Prov. Veragua: Macaraquito Camp (ANSP 22464-65); Zona del Canal: Ancon (MCZ 23870-72); Barro Colorado

Island (ANSP 24581; KU 75756, 117020); Cardenas (UF/FSM 29868); near Fort Clayton Reservation (UIMNH 41733); Fort Randolph (MCZ 18849); Fort Sherman (MCZ 26764); Howard Air Force Base (KU 117021); Isla Gigante (ANSP 24750); Summit (FMNH 83554). COLUMBIA: Depto. Antioquia: 4 km NE Bellavista, above Río Porce (FMNH 63756); Jericó, W of Medellín (AMNH 35243); Medellín (AMNH 35470, 35472, 35474-79, 35483; BMNH 97.11.12.14-15); Río Negrito, 15 km E Sonsón (FMNH 63757); Santa Rosa de Osas (AMNH 35781); Valdivia (FMNH 69659); Depto. Bolívar: Cartegena (FMNH 165193); Depto. Chocó: Camino de Yupe (LACM 72749); Condoto (BMNH 1910.7.11.32); Depto. Cundinmarca: La Mesa, near Bogotá (MCZ 46418); Sasaima (UMMZ 78264); near Bogotá (ZSM E4/1973); Depto. Magdalena: Santa Marta Mts. (UMMZ 54957); Depto. Meta: ≈ 15 km W Vista Hermosa (UTACV 3476); Depto. Nariño: Sandona (FMNH 54884); Tumaco (AMNH 20400); Depto. Santander: 42 km NW Bucaramanga, near Río Negro, Hac. "Berlin" (ZSM 96/1934-1-2); Depto. Valle: Cali (AMNH 4480); La Concepción (MCZ 6552).

Patterns C and D.—ARGENTINA: Prov. Buenos Aires: Buenos Aires (NMW 13813); Prov. Salta: Embarcación (LACM 73988). BOLIVIA: Depto. La Paz: Tumupasa [=Tumapasa] (AMNH 22504); Depto. Santa Cruz: Buenavista (CM 2823, 2826, 2908; FMNH 35642-43; ZSM E2/1973); La Perdiz (CM 2851) [not mapped]. BRAZIL: Est. Amazonas: Río Manjuru [=Rio Mamuru] (AMNH 101970-71); Río Purus (IRSNB 14918); Est. Goiás: Santa Isabel, Ilha de Bananal, Río Araguaia (AMNH 87965); Est. Mato Grosso: Chupada [=Chapada dos Guimaraes] (ANSP 11215); near Sao Cruz, road to Villa de Mato Grosso (CM 337); Tapirapé, confluence of Araguaia and Tapirapé rivers (AMNH 87964); Est. Pará: Belém (IRSNB 14915; KU 140178-79); 3 km E Belém (KU 128261); Santarém (AMNH 2841); Est. Río Grande do Norte: Extremoz (CAS-SU 6971); Est. Sao Paulo: Sao Paulo (MCZ 20805-06). BRITISH WEST INDIES: Tobago: no other data (MCZ 6337); Bacolet Guest House (AMNH 81447); 4 mi N Roxborough (RT 1221); Scarborough-Bacolet rd. burial ground (MCZ 56266); Trinidad: no other data (NMB 8993-94); Diego Martin (UF/FSM 16513); Guayaguayare (NMB 11363); Mt. Catherine (AMNH 64543); Piarco (FMNH 40445); Pointe-a-Pierre (MCZ 49068; UF/FSM 16768); Port-of-Spain (MCZ 8987, 87341, 126232); St. Ann's Ward, 7.5 mi N San Juan (RT 1217); San Raphael [=San Rafael] (FMNH 49970); Simla (AMNH 73092-93); Toco (AMNH 94888; MCZ 10138); Tucker Valley (AMNH 64473-74, 101341-42). COLOMBIA: Depto. Atlántico: mouth of Río Magdalena (NMW 20367); Depto. Meta: Lomalinda (UTACV 3717); Depto. Vaupés: Timbo (UTACV 3535); Gino-Goye, Río Apaporis (MCZ 53236). GUYANA: N Acarahy Mountains, W New River (KU 69836) [not mapped]; Dawa (ASFS 1002) [not mapped]; Georgetown (AMNH 36139); Kalacoon (AMNH 8099); Kartabo (AMNH 15147, 98216-17); Lama Creek, Demerara River (AMNH 36109) [not mapped]; Oko Mountains (FMNH 26667-68) [not mapped]; Paruima Mission (UMMZ 85292) [not mapped]; Placers de Carsevenne (MNHN 99-81) [not mapped]; between Wichabai and Isheartun (AMNH 60828). PARAGUAY: Depto. Cordillera: San Bernardino (ZSM 50/1925). SURINAM: no other data (MCZ 5394); Suriname Dist.: Powakka (CM 44323). URUGUAY: Depto. Tacuarembó: Banda (NMB 2118). VENEZUELA: Est. Aragua: Maracay (ZSM 136/1930); Est. Bolivár: Arabupu [=Arabopo] (UMMZ 85294-95); Guri (MBUCV III-1825); Mt. Roraima, Paulo side (UMMZ 85293); Río Uraricapará [=Río Uraicapa] (MBUCV III-8151); Est. Carabobo: Belén (MBUCV III-3142); Borburata (MBUCV III-8148); Dist. Federal: Caracas (NMB 11921); El Mamo (MBUCV III-3141); La Mariposa (MBUCV III-3842); Naiguata (CM 22774); Est. Mérida: Mérida (FMNH 4073; MCZ 17096, 17102; UMMZ 46620, 55901); Est. Falcón: El Mene (NMB 9236-37, 9982, 12862); Paují (MCZ 48762-65, 49033; NMB 13859); Riecito (NMB 13914); Est. Sucre: 24 km (by Puerto La Cruz Road) W Cumaná (KU 117056); Peninsula de Paria, Hac. Yacua (MCZ 43854).

Pattern E.—COLOMBIA: Depto. Amazonas: Leticia (MCZ 49003); Depto. Caldas: Laguneta (ANSP 25438); Depto. Cauca: El Tambo (ANSP 25428); Depto. Cundinmarca: near Bogotá (ZSM E4/1973); Depto. Putamayo: Putamayo, Río Putamayo (FMNH 37448). ECUADOR: Prov. Chimborazo: Riobamba (AMNH 23266, 23283); Prov. Morona: Gualaquiza (AMNH 25190); Miazal (USNM 198737); Prov. Napo: Concepción (USNM 198734); Lago Agrio (KU 126049-51); Limoncocha (LACM 73334; UIMNH 61257); headwaters of Río Arajuno, tributary Río Napo (USNM 198735); Santa Cecilia (KU 109848; MCZ 96667-68); Sarayacu (AMNH 28795); Prov. Pas-

taza: Alto Río Curaray (USNM 198717, 198722) [not mapped]; Canelos (AMNH 49060-61; NMW 20366:3-4; USNM 198721); Mera (KU 98624, 121342); Puyo (USNM 198715); Río Corrientes (USNM 198720); Río Pindo, near village of Río Tigre (USNM 198716) [not mapped]; Río Villano (USNM 198718-19); Prov. Santiago: Río Upano (AMNH 28813). PERÚ: Depto. Amazonas: upper Río Nieva (AMNH 55887); Depto. Ayacucho: Sivia, on Rio Apurímac (FMNH 39645); Depto. Cuzco: Marcapata (FMNH 59173-74, 62128); Depto. Huanuco: [Rio] Pachitea (AMNH 52683); ≈ 35 km NE Tingo María (LSUMZ 25441); Depto. Junín: La Merced (ZSM 138/1930-1-4); Depto. Loreto: Centro Unión (TCWC 38209, 39123, 40532, 41436, 44105); Iquitos (AMNH 52496, 52753, 53122, 53164, 54891, 56121); Lago Mirano, lower Río Napo (AMNH 53310); Mishana (TCWC 38206-08, 44106); Monte Carmelo (Requena) (AMNH 55928); Nanay (AMNH 52496); Pampa Hermosa (AMNH 53562, 55440, 55759, 55768, 55859, 55894, 55966); Panya, Río Cushabatay (AMNH 52353); Pevas (CAS-SU 12497); Río Curanja [=Río Curanga], Balta (LSUMZ 14595); Río Samiria and Parinari Cañon (AMNH 57265); mouth of Río Santiago (AMNH 52687, 53251); Roaboya (AMNH 52476, 52480, 53093); Tipishca (Contamana) (AMNH 52172); Yarinococha, Río Ucayali (FMNH 56125); Depto. Pasco: Huancabamba (NMW 20363:1-3); Depto. San Martin: Río Ponasa (AMNH 52820); Tocache (AMNH 52391).

Pattern F.—ECUADOR: Prov. Esmeraldas: Quininde [=Rosa Zarate] (NMW 20366:2); Prov. Guayas: Guayaquil (ANSP 3353); Prov. Loja: Loja (USNM 198736); Prov. Pichincha: Chiriboga (USNM 198733); Memé (USNM 198729); below Pacto (USNM 198731); Quito (ANSP 24777); Río Baba, 19 km S, 5 km E Santo Domingo de los Colorados (UIMNH 92236-37); Río Baba, 24 km S Santo Domingo de los Colorados (UIMNH 92238); Río Toachi, 5 km N, 1 km E Santo Domingo de los Colorados (UIMNH 92239) [not mapped]; 4 km E Río Baba "bridge," 24 km S Santo Domingo de los Colorados (UIMNH 92240); Santo Domingo de los Colorados (NMW 20366:1; MCZ 147302; USNM 198723-25, 198728); below Sigchos (USNM 198730).

Key to the Members of the *Tantilla melanocephala* Group

1. Nuchal spots confluent with dorsal body ground color; no dark nape band; dorsal ground color pale with diffuse dark stripes on middle of row 1, upper half of 2 and lower half of 3, middle of 4, upper half of 5 and lower half of 6; middorsal dark stripe well-defined, present on middorsal scale row, connected to dark markings along medial edge of paravertebral scales . . . *T. insulamontana*
   Color pattern not as above 2

2. Dorsal ground color pale with bold dark stripes on middle of row 1, upper half of row 2 and lower half of row 3, upper edge of row 4 and lower middle portion of row 5, middle of row 6, and the middle of the middorsal scale row; preocular spot continues posteriorly onto preocular scale to touch eye . . . . . *T. equatoriana*
   Color pattern not as above 3

3. Dorsum of head with much pale pigment, consisting of extensive pale markings on snout continuing posteriorly over supraocular and anterolateral corner of parietal and downward to connect with the postocular pale spot; dorsal pattern consisting of dark middorsal stripe confined to middorsal row and pale lateral stripe confined to upper half of row 3 on a pale ground color . . . *T. andinista*
   Color pattern not as above 4

4. No dark middorsal stripe 5
   Dark middorsal stripe present 6

5. Pale nuchal band complete or divided medially; pale neck band following dark nape band . . . . . *T. capistrata*
   Pale nuchal band usually divided both medially and laterally; no pale pigment following dark nape band . . . . . *T. melanocephala* (**pattern C**)

6. Dark pigment bounding pale neck band posteriorly 7
   No dark pigment bounding pale neck band (if present) posteriorly 8

7. Nuchal spots distinct and usually restricted to parietal scales; no dark ventral border of pale lateral stripe (if present); lateral extension of dark head cap separating postocular pale spot and pale pigment on lateral gulars (opposite pale nuchal spots) . . . . . *T. melanocephala* (**pattern A**)
   Nuchal spots indistinct and largely confined to scales posterior to parietals; dark ventral

border of pale lateral stripe present; no lateral extension of dark head cap separating postocular pale spot and pale pigment on lateral gulars (opposite pale nuchal spots) ..... *T. lempira*

8. Middorsal stripe poorly developed, diffuse, often broken; pale lateral band usually absent, but, if present, not bounded by dark pigment ..... *T. melanocephala* (**pattern D**)
   Middorsal stripe well-developed, complete; pale lateral band usually present and bounded above and/or below by dark pigment 9

9. Dark nape band well-developed, well-distinguished from ground color of head and body; pale nape band usually present and not reduced in extent ..... *T. melanocephala* (**pattern E**)
   Dark nape band usually poorly developed, barely distinguishable from ground color of head and/or body; pale neck band posterior to dark nape band usually reduced to small spots on either side of middorsal dark stripe or absent 10

10. Lateral extension of dark head cap separating postocular pale spot and pale pigment of lateral gulars (opposite pale nuchal spots) present; color of dorsum of head essentially the same as that of the dorsum of body ..... *T. melanocephala* (**pattern F**)
    Lateral extension of dark head cap separating postocular pale spot and pale pigment of lateral gular (opposite pale nuchal spots) absent; color of dorsum of head paler than that of dorsum of body ..... *T. melanocephala* (**pattern B**)

Distributional Patterns

Geographic patterns.—The most striking aspect of the geographic distribution of the members of the *Tantilla melanocephala* group is the wide range of the nominate species and the peripheral or virtually peripheral ranges of the remainder of the species. As herein interpreted, *Tantilla melanocephala* has the widest range of any species in the genus, occurring from Guatemala south to southern Perú, Bolivia, northern Argentina, and Uruguay. The other 5 species are scattered along the edges of the range of the central species, apparently in habitats that are marginal for or outside the habitat span of *T. melanocephala*.

Tantilla lempira sits almost at the northern extremity of the range of the group and occupies the upland pine forests along the Pacific versant of Honduras. Because much of the interior of Honduras is covered by such forest, perhaps *T. lempira* has a much larger range in the country than is now known.

Two species, *T. andinista* and *T. insulamontana*, occur in relatively isolated high intermontane basins in the Andean chain in Ecuador. *Tantilla andinista* is known only from the Alausí Basin and *T. insulamontana* from the Jubones Basin. Both of these basins or *hoyas* are drained by rivers that flow into the Pacific and the Pacific slope of Ecuador is sparsely populated by members of the *Tantilla melanocephala* population system (only members of pattern type F).

Tantilla equatoriana occurs in extreme northwestern Ecuador. This area is covered by rain forest (Savage, 1960) and it is not immediately apparent why *T. melanocephala* does not occur in this area, so far as is known, because it occurs across the border along the Pacific coastal plain of Colombia. Perhaps more collecting in northwestern Ecuador will demonstrate the existence of *T. melanocephala* there.

Tantilla capsitrata occupies the hostile coastal deserts and the semiarid inter-Andean basin formed by the valleys of the upper Río Marañon, Río Chinchipe and Río Chamaya in northwestern Perú. Again the area appears to be inhospitable to the more mesic-adapted *T. melanocephala*.

As mentioned above, *T. melanocephala* is wide-ranging and a centralized member of the group. In Central America it occupies both subhumid (pattern A) and humid (pattern B) environments. In northern Central America (Guatemala to Nicaragua) the species occurs primarily along the Pacific versant, whereas in lower Central America (Costa Rica and Panamá) it is widely distributed on both versants. In South America it appears to occur in any habitat in the portion of the continent east of the Andes as far south as the humid pampa that is sufficiently humid and low in elevation. It also occurs along the lower western flank of the Andes in northwestern Ecuador and in the lowland and riverine fingers that interdigitate with the 3 cordilleras in Colombia.

Physiographic patterns.—As might be predicted by its extensive geographic distribution, *Tantilla melanocephala* inhabits a wide range of physiographic types. In Central America, pattern

A individuals principally occupy the Pacific coastal plain but also range into the lower elevations of the Pacific slopes of the central mountain ranges (range in elevation sea level to 1450 m). Although principally occurring on the Pacific versant, pattern A individuals are known to occur on the eastern side of Lake Nicaragua on the Caribbean side.

Pattern B individuals occur in the Atlantic lowlands in Nicaragua (?) and Costa Rica. They also occur along the Pacific lowlands and the foothills of southwestern Costa Rica and western Panamá. They have been collected at elevations ranging from 30 to 762 m.

The intermediate specimens in Panamá occupy the lowlands in the area of the Canal Zone and the Pacific lowlands of the eastern portions of the country at elevations not exceeding 600 m.

In Colombia the intermediate specimens occur principally in the lowland region (Atlantic and Pacific) and in the river valleys which divide the 3 cordilleras (Cordillera Occidental, Cordillera Central, and Cordillera Oriental) from one another. The Atlantic coastal specimens are from elevations near sea level, with the exception of a specimen from the Santa Marta Mountains, which came from an unknown locality. Ruthven (1922) mentioned specimens, which we have not seen, from Cerro San Lorenzo and Palomina at elevations, respectively, of 1220 and 1525 metres. He also mentioned specimens from Fundación and Valencia, which are on either side of the main mass of the Santa Marta Mountains but gave no elevation for either. The specimens from the Pacific coastal region are from the Serranía de Baudó at an elevation of 420-625 m, the valley of the Río San Juan near the southern end of the Serranía de Baudó, and from sea level along the southwestern Pacific lowlands. The latter specimen shows no resemblance to the 2 known specimens of *Tantilla equatoriana*, although the localities whence they came are but approximately 70 airline kilometres apart and covered with presumably the same type of vegetation. Specimens from the Colombian Andes have come primarily from the rift valleys between the 3 cordilleras. These 3 mountain ranges merge at their southern ends but separate at the northern end providing a relatively low elevation dispersal route for Atlantic coastal animals into the Colombian Andes. *Tantilla melanocephala* has been recorded from this area at elevations as low as 135-180 m at the northern end of the cordilleras to 2801 m in the Medellín Valley.

Tantilla melanocephala also occurs along the narrow Caribbean coastal plain in Venezuela from the area east of the Segovia Highlands to that north of the mountains of the northern range of the Central Highlands northeast of the valley of Caracas at elevations not exceeding 152 m. It also occurs in the Mérida Basin along the Río Chama at an elevation of 1640 m in the Cordillera de Mérida. In the Central Highlands it occurs in both the northern and southern ranges and in the valleys that separate them (valley of the Río Tuy, valley of Caracas, and the Valencia Basin) at elevations ranging from 305-1000 m. The species also inhabits the Northeastern Highlands from the mountains southwest of the Golfo de Cariaco to the Paria Peninsula.

Tantilla melanocephala is also found on the islands of Trinidad and Tobago, geologically part of South America. The species is widespread on Trinidad, occurring in most (if not, in fact, all) of the physiographic divisions of the island. It has been recorded from the area of the Northern Range at elevations from near sea level to 457 m. It occurs in the northern lowland belt along the Caroni and Talparo rivers (one of 2 localities from this region is at ≈ 14 m). In the southern lowland belt specimens have been found along the western coast at or near sea level. Specimens from the region of the southern highlands are from the southeastern coast at or near sea level.

Back on the mainland, *Tantilla melanocephala* has been recorded from the eastern portion of the Orinoco llanos. The species has also been found in the eastern and extreme western portions of the Guiana highlands in, respectively, southeastern Venezuela (at or near 305 m) and southern Guyana, on the one hand, and in southeastern Colombia, on the other. Its lack of occurrence in the central portions of the Guiana highlands is due, no doubt, to insufficient collecting. Northeast of the Guiana highlands is a coastal plain where *T. melanocephala* also occurs in Guyana and Surinam (no records are available for French Guiana but the snake undoubtedly occurs there).

Occurrence of *T. melanocephala* in the alluvial plain of the Río Amazonas is also documented. Near the mouth of the river it has been found at elevations of 12 m and farther upstream at 20 m near Santarém. In the upper drainage of the Amazon Basin the distribution is better known. It occurs in the Amazon lowlands of southern Colombia, eastern Ecuador, and eastern Perú from elevations as low as 84 m in southeastern Colombia, into the eastern flanks of the Andes in

Ecuador up to 1020 m and along the valleys and tributaries of the Ucayali, Huallanga and Madre de Dios rivers in the eastern Peruvian Andes up to 3080 m. The species also occurs in the southern extension of the Amazon Basin along the Río Grande in eastern Bolivia (823 m) and along the base of the front range of the Bolivian Andes (457-610 m).

In the vast region of the Brazilian highlands *T. melanocephala* has been sparsely but so widely collected that we can say that it probably occurs in much of the area. It has been recorded from the coastal plain of northeastern Brazil, Ilha de Bananal, Matto Grosso Plateau, the Serra do Mar, Paraná Plateau, and the Uruguayan highlands.

Tantilla melanocephala also is found in the Gran Chaco and in the Humid Pampa, the latter being the southernmost physiographic province in which the species is known to occur.

Finally, although most of the distribution of *T. melanocephala* is east of the Andean chain, the species also occurs west of the Andes in the Guayas lowland (at sea level) and the coastal hilly belt (600-1863 m) in Ecuador. It also is found in the intermontane basins of Quito (2851 m), Riobamba (2700 m), and Loja (2200 m).

The other species of the *melanocephala* group occur in areas outside of the range of *Tantilla melanocephala. Tantilla lempira* is distributed in the eastern portion of the southern cordillera of the serranía region of Honduras (*sensu* Meyer, 1969). *Tantilla equatoriana* has been found only in the coastal lowlands north of the coastal hilly belt in Ecuador. *Tantilla andinista* is known from the Alausi intermontane basin at an elevation of 2600-2750 m. *Tantilla insulamontana* occurs in the Jubones intermontane basin at known elevations of from about 1250-2100 m. *Tantilla capistrata* is distributed along the northern coastal plain of Perú and in the valleys of the Marañon, Chinchipe, and Chamaya rivers in north-central Perú.

Phytogeographic patterns.—Little direct evidence of the types of vegetation inhabited by members of the *Tantilla melanocephala* group is available. What follows is an effort to reconstruct a phytogeographic picture for the group from information provided by a wide variety of sources. It must be acknowledged at this point that it is difficult to reconcile the various systems that have been used to describe the vegetational patterns of different areas within the range of the *melanocephala* group. We have tried to apply the Holdridge (1964) system of vegetatonal formations as broadly as possible but have found it difficult to do so in some cases due to lack of sufficient information and have reverted to other, less precise sorts of descriptions.

In Central America, individuals belonging to the pattern A grouping are principally distributed in the Tropical Dry Forest formation (in El Salvador, Honduras, Nicaragua, and Costa Rica) but they also extend marginally into the Subtropical Moist Forest formation in Guatemala, Nicaragua, and Costa Rica, the Subtropical Wet Forest formation in Guatemala, and the Tropical Moist Forest formation in Costa Rica.

Pattern B individuals are widely distributed in wet forest types, occurring in Tropical Wet Forest, Subtropical Wet Forest and Subtropical Rain Forest formations in Costa Rica and in the Subtropical Wet Forest formation in Panamá.

The intermediate specimens in Panamá came principally from the Tropical Moist Forest formation but also from the Tropical Dry Forest formation.

Tantilla melanocephala is widely distributed in South America and, as such, inhabits many of the vegetational types found on that continent east of the Andean chain and south to the Pampas. In Colombia the intermediate individuals have been found in 3 areas: (1) the Atlantic coastal plain; (2) the Pacific coastal area; (3) the rift valleys between and the lower slopes of the Colombian Andes. The Atlantic lowlands of Colombia are in Holdridge's Tropical Thorn Forest formation or thorn scrub. Along the Pacific coast of Colombia the snake occurs in the Tropical Wet Forest formation or tropical lowland rain forest. In the rift valleys between the 3 cordilleras of the Colombian Andes, *Tantilla melanocephala* occurs at lower elevations in the Tropical Moist Forest formation and at higher elevations in formations presumably ranging from Subtropical Moist Forest through Lower Montane Moist Forest and into Montane Wet Forest.

Moving eastward from western Colombia, *T. melanocephala* ranges along the Venezuelan coastal plain into the strip of thorn scrub (Tropical Thorn Forest formation) that is an extension of that along the Caribbean coastal plain of Colombia. It also occurs in the Lower Montane Moist Forest formation in the Mérida Basin in the Cordillera de Mérida. In the Central Highlands of Venezuela, the species ranges into the Subtropical Dry Forest formation.

On Trinidad the eastern coast receives from

2540-3810 mm of rainfall. The rainfall decreases toward the west to between 1270 and 1524 mm along the west coast (James, 1959). The eastern portion of Trinidad would fall within Holdridge's (1967) Tropical Moist Forest formation (quasi-rain forest) and the western coast within the Tropical Dry Forest formation. *Tantilla melanocephala* occurs virtually throughout the island.

Tantilla melanocephala has also been recorded in the eastern portion of the Orinoco llanos, an area of grassland with "semideciduous trees growing singly or in groups or patches" (Uzzell, 1973). In the Holdridge system the area would fall in his Tropical Arid Forest formation, a slightly misleading application. In the Guiana Highlands the species occurs in the Tropical Moist Forest and Tropical Wet Forest formations.

Along the coastal plain of the Guianas *T. melanocephala* occurs in the Tropical Moist Forest formation. In the lower Amazon alluvial plain the species is distributed in the Tropical Moist Forest and Tropical Dry Forest formations. In the upper drainage it occurs principally in the Tropical Moist Forest formation but also in the Subtropical Wet Forest formation of the eastern flanks of the Ecuadorian and Peruvian Andes.

In the Brazilian highlands *Tantilla melanocephala* has been found in the *caatinga*, the thorny deciduous woodland of northeastern Brazil, and the woodland savanna of central Brazil. Along the coast of southeastern Brazil it occurs in the Tropical Moist Forest formation, in tropical lowland rain forest or in luxuriant semideciduous forest (James, 1959).

In the Uruguayan highlands *T. melanocephala* occurs in tall-grass prairies and in Paraguay in tropical semideciduous forest. In Argentina the species has been found in the vast grass-covered plain of the Humid Pampa and in the deciduous scrub forest interspersed with patches of grassy savanna known as the Gran Chaco.

The ecological distribution of *T. melanocephala* in Bolivia is not clear but it appears that the species may occur in the arm of *selva* that extends south along the front ranges of the Bolivian Andes or in the palm savanna to the east of there.

On the Pacific side of Ecuador *Tantilla melanocephala* is distributed in the deciduous broadleaf forests in the Guayas lowlands, in the Subtropical Moist Forest formation or premontane rain forest of the coastal hilly belt, and in the Montane Moist Forest formation or montane grasslands of the Quito and Riobamba basins and the semiarid vegetation (Montane Dry Forest formation) of the Loja basin.

Tantilla lempira occurs in the Subtropical Moist Forest formation (*Pinus oocarpa* forest) in south-central Honduras. *Tantilla equatoriana* occurs in the Tropical Moist Forest formation of coastal northwestern Ecuador. *Tantilla andinista* is found in the montane grasslands of the Alausi basin. *Tantilla insulamontana* is known only from the Jubones basin which supports semidesertic vegetation (Acosta-Solis, 1966). Arthur C. Echternacht, who collected the holotype informed me (*personal communication*) that "the valley of the Rio Jubones is increasingly drier as one moves east from the coast, and was quite dry at the Rio Minas." *Tantilla capsitrata* occurs in the hostile barren coastal desert of northwestern Perú and the semiarid inter-Andean valleys of the Marañon, Chinchipe and Chamaya rivers. The extremely arid coastal desert results from a rain-shadow effect produced by a combination of the effects of the Andes to the east and the cold-water Humboldt Current offshore (Dixon and Wright, 1975). The inter-Andean valleys of north-central Perú lie in a ". . .rain shadow formed by the eastern front ranges of the Andes" (Dixon and Wright, 1975). Dixon and Wright (1975) noted 3 plant formations characteristic of the coastal desert: (1) desert—an area with no or only isolated plants; (2) lomas—isolated, elevated hills frequently shrouded with fog and supporting ephemeral herbs; (3) riparian communities—trees, shrubs, and herbs growing adjacent to streams having their origin high in the Andes. Although we have no direct evidence about which of these plant formations *T. capistrata* inhabits it seems more likely that they would occur in the riparian areas. Dixon and Wright (1975) described the nonriparian vegetation of the inter-Andean valleys as consisting of "thorn scrub with mesquite *(Prosopis)*, paloverde *(Cercidium)*, and columnar cactus *(Cereus* and *Cephalocereus)* dominating."

Relationships and Evolution

Study of interspecific relationships within the *melanocephala* group of the genus *Tantilla* has been hampered by the small sample size of most of the species herein recognized, which precluded examination of internal characters. At any rate,

internal characters have not been subjected to analysis in the genus as a whole. This is a subject the senior author hopes to take up in future papers. Thus, we have been limited in attempting to assess relationships to consideration of external characteristics. It is the characteristics of the pattern that appear to be most useful in this regard, inasmuch as the characters of scutellation are either relatively invariable or too variable.

Relationships.—The pattern character states common to all members of the *melanocephala* group are as follows: (1) dark head cap present; (2) pale marking present on nuchal area; (3) preocular pale blotch present; (4) postocular pale blotch present. Some of the remainder of the pattern character states are so distributed that small clusters of pattern groupings are apparent. The pattern grouping clusters and the significant features shared in common are as follows:

A. *Tantilla melanocephala* (**pattern A**)—*T. lempira:* little, if any, distinction in intensity of color between dark head cap and dark nape band; pale pigment on snout restricted to dorsal apex of rostral and anteromedial portion of internasals; nuchal spots small, well-separated from dorsal extension of pale gular color; pale neck band present; dorsal ground color tan to pale brownish-gray; middorsal dark stripe narrow, confined to middle of middorsal scale row; pale lateral stripe confined to upper portion of dorsal scale row 3 and lower portion of 4.

B. *Tantilla equatoriana*—*T. insulamontana:* nuchal spots relatively large, present on posterior portion of parietals and postparietal scales; middorsal stripe extends onto paravertebral scales; dark stripe through middle of dorsal scale row 1; dark stripe on upper half of scale row 2 and lower half of 3; pale lateral stripe on upper portion of scale row 3 and lower portion of 4; dorsal scale rows 4, 5, and 6 with dark striping; pale dorsolateral field extending from upper half of scale row 6 to lateral apex of scales of middorsal row.

C. *Tantilla melanocephala* (**pattern C and D**)—*T. melanocephala* (**pattern E**): dark head cap paler in color than dark nape band; pale pigment present on internasals and prefrontals; pale nuchal band medially divided; pale neck band present; pale lateral stripe, if present, relatively broad, usually occupying the upper half of scale row 3 and all of 4.

The remainder of the pattern groupings are such that the number of distinctive pattern features outweigh those held in common with any other taxon or pattern group. These pattern groupings and their distinctive suites of pattern character states are as follows:

A. *Tantilla melanocephala* (**pattern B**).—dark head cap much paler in coloration than dark nape band; no pale pigment on snout; pale nuchal spots often not present; dark nape band sometimes not distinguishable from dorsal ground color; pale neck band usually absent; dark subocular blotch, if present, poorly developed, consisting of dark pigment along suture lines between supralabials 3, 4, and 5; lateral extension of dark head cap usually absent; pale lateral stripe relatively broad, usually occupying the upper half of scale row 3 and all of 4 or the upper half of 3, all of 4, and the lower half of 5.

B. *Tantilla melanocephala* (**pattern F**).—usually no distinction between the color of the dark head cap and dark nape band, which in turn is usually not distinguishable from the dorsal ground color; no pale pigment on snout; pale nuchal spots muted, occupying the posterior portion of the parietals and postparietal scales; pale neck band either absent or confined to one or two scales on either side of the dark middorsal stripe.

C. *Tantilla andinista.*—extensive pale markings on the internasals, prefrontals, supraoculars, and parietals; pale nuchal band broad and medially divided; pale lateral stripe narrow, confined to upper half of row 3.

D. *Tantilla capistrata.*—dark head cap same color as dark nape band, which both are much darker than the dorsal ground color; snout to level of anterior half to three-quarters of prefrontals pale in color; nuchal band well-defined, medially divided or complete; dorsum pale in color, with no dark middorsal stripe or only slight indication of one; no pale lateral stripe.

These groupings seem to point to relatively close genetic relationships between those pattern groupings showing a high number of shared character states, on the one hand, and more distant relationships of those having a high number of distinctive character states with any other pattern grouping, on the other.

Further analysis reveals that the pattern B, E, and F specimens of *T. melanocephala* resemble one another in having a relatively dark dorsal ground color, a well-defined middorsal dark stripe, a well-defined, contrasting, relatively broad lateral pale stripe, usually occupying at least the lower half of scale row 3 and all of 4. In addition, *T. capistrata* resembles patterns C and

D specimens of *T. melanocephala* in having an indistinct middorsal dark stripe (if any), a relatively pale dorsal ground color, no pale lateral stripe and a well-defined medially divided or complete pale nuchal band. A close evolutionary relationship between the members of the latter group is equivocal given the differences in habitat and the degree of isolation from one another (but see below). *Tantilla andinista* remains a distinctive isolate.

Evolutionary trends.—A worker attempting to construct a phylogeny based on an analysis of evolutionary trends determined by changes in pattern character states is treading on thin ice indeed. Nonetheless, we have made an effort to do so, risking a fall into the cold water of sceptical criticism. Following the arrangement used by Savage (1975), we have ranked below each of the important character states discussed as primitive (P), intermediate derived (I), or advanced (A). Where the character state trends are multidirectonal they are listed as i, ii and iii:

	P	I	A
middorsal stripe	i) well-developed	reduced	absent
	ii) well-developed		broadened
pale lateral stripe	well-developed	reduced	absent
dorsolateral field	uniform		striped
dark head cap	i) uniform	pale snout	*andinista* pattern
	ii) slightly paler		much paler than dark nape band
	iii) slightly paler		same color as dark nape band
pale nuchal band	i) medially divided	small spots	absent
	ii) medially divided		complete
subocular blotch	well-developed		reduced
lateral extension of dark head cap	present		absent
pale neck band	well-developed	reduced	absent
dark nape band	i) present		absent
	ii) distinct from ground color		not distinct

This disposition of character states suggests that the basic evolutionary stock of the *Tantilla melanocephala* group possessed the following features: middorsal stripe well-developed; pale lateral stripe well-developed; dorsolateral field uniform in color; dark head cap slightly paler than the dark nape band; no or few pale markings on the snout; pale nuchal band medially divided; subocular blotch well-developed; lateral extension of the dark head cap present; dark nape band present and darker than ground color; pale neck band well-developed.

The above description fits perfectly members of the pattern E group of *Tantilla melanocephala.*

Evolutionary model.—The data derived from a study of evolutionary trends in color and pattern indicate that the pattern E group, located in the upper reaches of the Amazon basin, is closest to the postulated basal evolutionary stock of the *melanocephala* group. The pattern C-D group, occupying the bulk of the South American range of the species, appears to be the most recent offshoot of the basal stock, differing from the pattern E group in having a paler ground color with less well-developed (or nonexistant) middorsal dark stripe and pale lateral stripe. Another level of evolutionary change is represented by pattern F and pattern B specimens. Each of these pattern groups presently has a relictual distribution, pattern B in the humid lowlands of Nicaragua, Costa Rica and western Panamá and pattern F along the western flanks of the Ecuadorian Andes. A third level of differentiation is represented by the pattern A group and *T. lempira*, both occurring at

the northern extremity of the range of the *melanocephala* group. The principal distinction of this group is the reduction of the pale nuchal band to 2 spots near the posterior end of the parietals and the lack of distinction between the ground color of the head and the color of the dark nape band.

The relationships of *T. capistrata* appear to lie most closely with the pattern C-D grouping of *T. melanocephala*. They agree in having a poorly developed dark middorsal stripe (or none at all), in having no pale lateral stripe (usually) and in having a medially divided or complete (in *T. capistrata*) pale nuchal band. *Tantilla capistrata* remains a distinctive isolate, however, in the deserts of northwestern coastal Peru and the arid intermontane valleys of the area around the Porculla Pass in north-central Peru. A hypothesis to account for the present isolation of these 2 groups and their separation by populations of the pattern E group of *T. melanocephala* is offered in the succeeding section.

Tantilla andinista is a distinctive isolate in the Alausí intermontane basin in central Ecuador. It appears to have no close relatives within the group which means that it may be a remnant of a coastal Ecuadoran population no longer extant or as yet undiscovered.

The last spectrum of evolutionary differentiation is represented by the species *T. equatoriana* and *T. insulamontana*, both occurring as isolates on the Pacific versant of Ecuador. The distribution of neither is well understood but presently they are well-separated geographically and altitudinally from one another. They resemble one another in having a multilineate pattern and a broad dark middorsal stripe. They differ from one another principally in that *T. insulamontana* lacks a dark nape band. These 2 species appear to be early offshoots from the basal evolutionary stock of the group and to have diverged from one another relatively early in the evolutionary history of the group.

Evolutionary history.—There is ever-increasing information to indicate that the significant events in the evolutionary history of many recent groups of South American vertebrates has taken place within relatively recent times in the Pliocene, Pleistocene and Holocene epochs. In addition, this same evidence points to a succession of several alternating arid and humid climatic phases during which there occurred alternate contractions and expansions of closed canopy forest and open savanna or thorn forest formations (van der Hammen, 1961; Haffer, 1969; Vanzolini and Williams, 1970; Vuilleumier, 1971; Duellman, 1972; Heyer, 1973; Duellman and Crump, 1974).

The conclusions arising from this evidence are in marked contrast to the traditional view of long-term stability of the South American rain forest (Darlington, 1957; Schwabe, 1969), on the one hand, and the antiquarian view of the biogeographic history of the Central American herpetofauna (Duellman, 1958; Savage, 1966, 1975; Wilson and Meyer, 1971), on the other. These disparities were pointed out by Myers (1974).

The evidence concerning the evolutionary and distributional relationships of the members of the *Tantilla melanocephala* lends support to a hypothesis of the occurrence of marked arid-humid climatic fluctuations in the Quaternary.

As pointed out by Savage (1975), "the test of any phylogenetic model is to compare the evolutionary divergences and relations of the studied group against the known environmental history of the geographic region where the group occurs."

We submit the following evolutionary model to account for the present-day evolutionary relationships:

1. Movement of the basal evolutionary stock of the *Tantilla melanocephala* group into South America following the reemergence of the isthmian link connecting Middle and South America at the beginning of the Pliocene (Savage, 1966).

2. Early evolution of the basal stock in the lowland forest in the upper Amazon region (Haffer, 1969).

3. Isolation of the *T. equatoriana—insulamontana* stock along the west coast of South America by the uplift of the Andes in the upper Pliocene and lower Pleistocene (Haffer, 1969).

4. Isolation, perhaps, of the *T. andinista* stock in an intermontane basin during this same period of Andean orogeny. Another alternative is that the *T. andinista* stock moved into the presently semiarid Alausí Basin from the Pacific coastal lowlands during an interglacial arid period subsequent to the Andean orogeny and became isolated subsequently during the next glacial pluvial period.

5. Movement of the pattern A—*T. lempira* stock into Central America during an interglacial arid phase.

6. Isolation of the pattern F stock and pattern B stock in the Chocó and Nechi forest refuges of

Haffer (1969), respectively, perhaps, during the same interglacial period that allowed for the northward movement of the pattern A-*T. lempira* stock.

7. Movement of the pattern C-D stock through the Amazon Basin presumably during a pluvial glacial phase. Perhaps, during this period the pattern B group was able to expand its range into humid environments along the Atlantic coast of lower Central America and the pattern F group into similar environments along the western slopes of the Ecuadoran Andes.

8. Movement of the *T. capistrata* stock into the arid Pacific lowlands of northwestern Perú and the area of the Porculla Pass during an arid phase and its subsequent isolation during the establishment of the present patterns of vegetational distribution. Also at this time the patterns A and B group came into secondary contact and these in turn with the South American pattern groups to produce the current picture of distribution in northwestern South America.

The above explanation of the evolutionary history of the *melanocephala* group corresponds well with that presented by Duellman and Crump (1974) for the *Hyla parviceps* group even though that group's distribution is cis-Andean exclusively. It also corresponds well with data presented on Quaternary climatic changes in South America (van der Hammen, 1961; Haffer, 1969, 1970; Vuilleumier, 1971). However, it is uncertain which of the postulated major dry-humid alternation sequences during the Pleistocene or the more minor, less severe ones during the Holocene are correlated with the above-detailed evolutionary events.

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Division of Intercurricular Studies, Miami-Dade Community College, South Campus, Miami, Florida 33176 and 1561 S.W. 12th Avenue, Miami, Florida 33129.

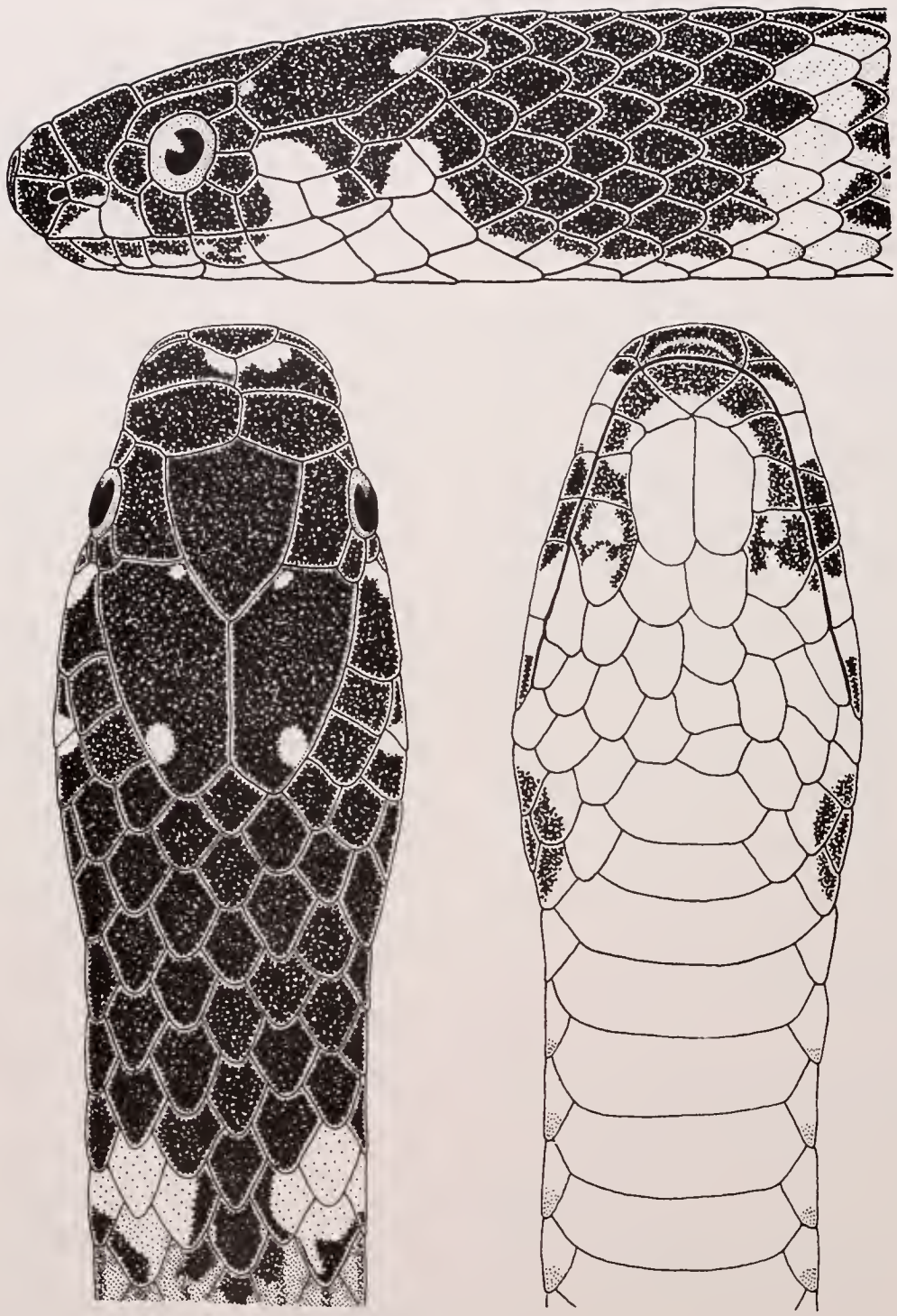


Fig. 1. Lateral, dorsal, and ventral views of head of a member of the pattern A group of *Tantilla melanocephala* (KU 102529, Finca Taboga, ≈ 20 km SE Las Cañas, Prov. Guanacaste, Costa Rica). All figures are drawn on a generalized scale pattern.

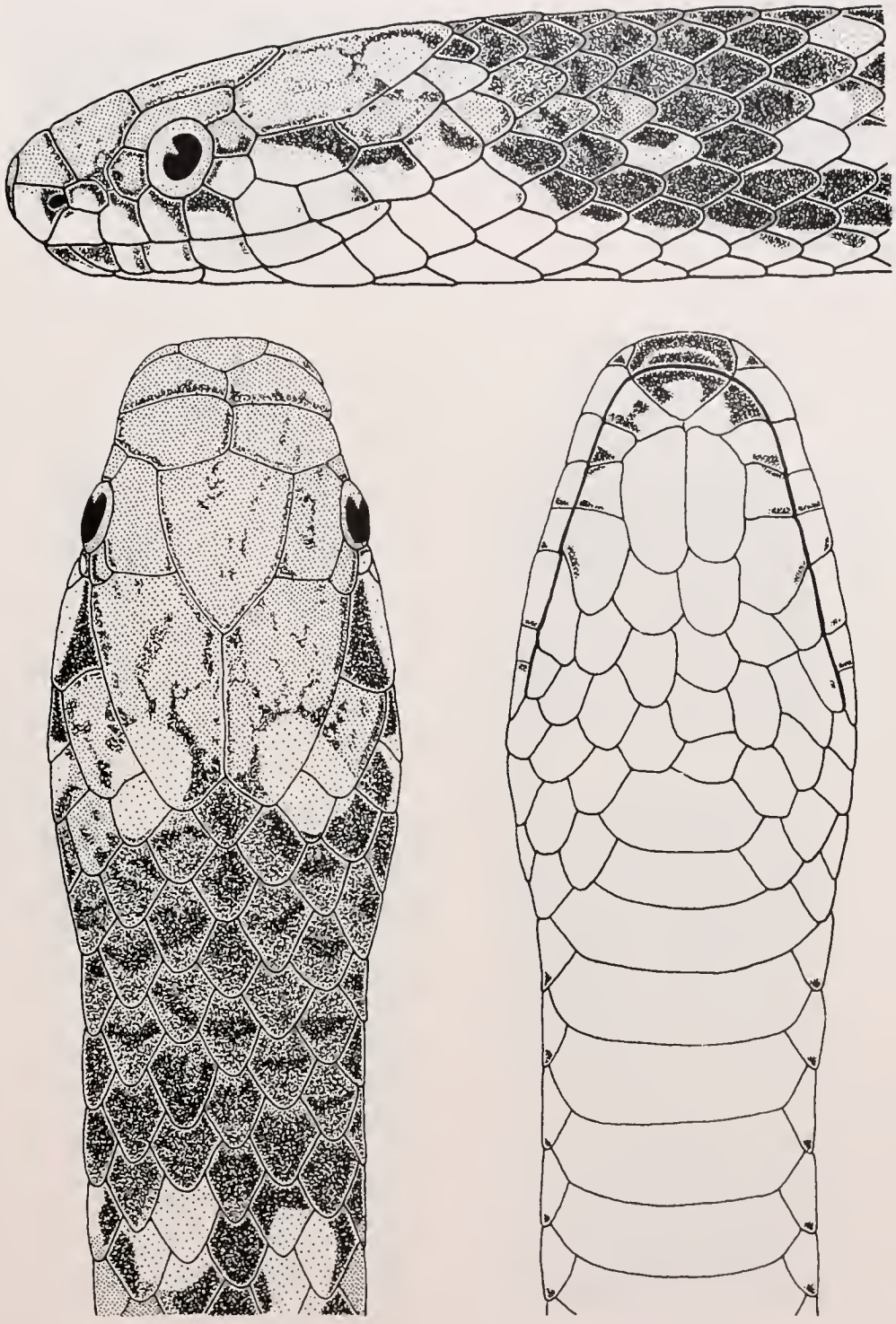


Fig. 2. Lateral, dorsal, and ventral views of head of a member of the pattern B group of *Tantilla melanocephala* (KU 31960, 16 km NW San Isidro el General, Prov. San José, Costa Rica).

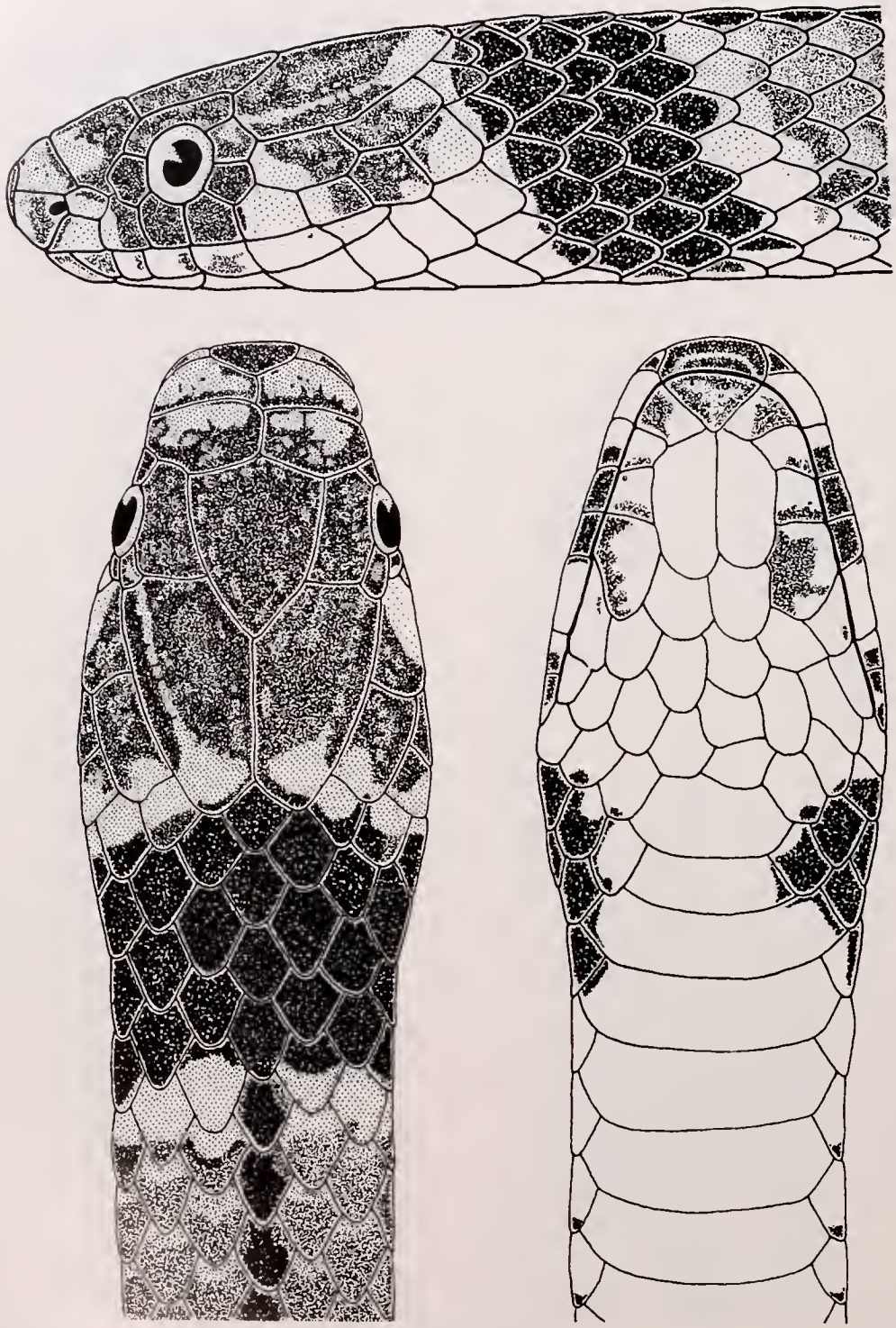


Fig. 3. Lateral, dorsal, and ventral views of head of a member of the pattern D group of *Tantilla melanocephala* (MBUCV III-1825, Guri, Est. Bolívar, Venezuela).

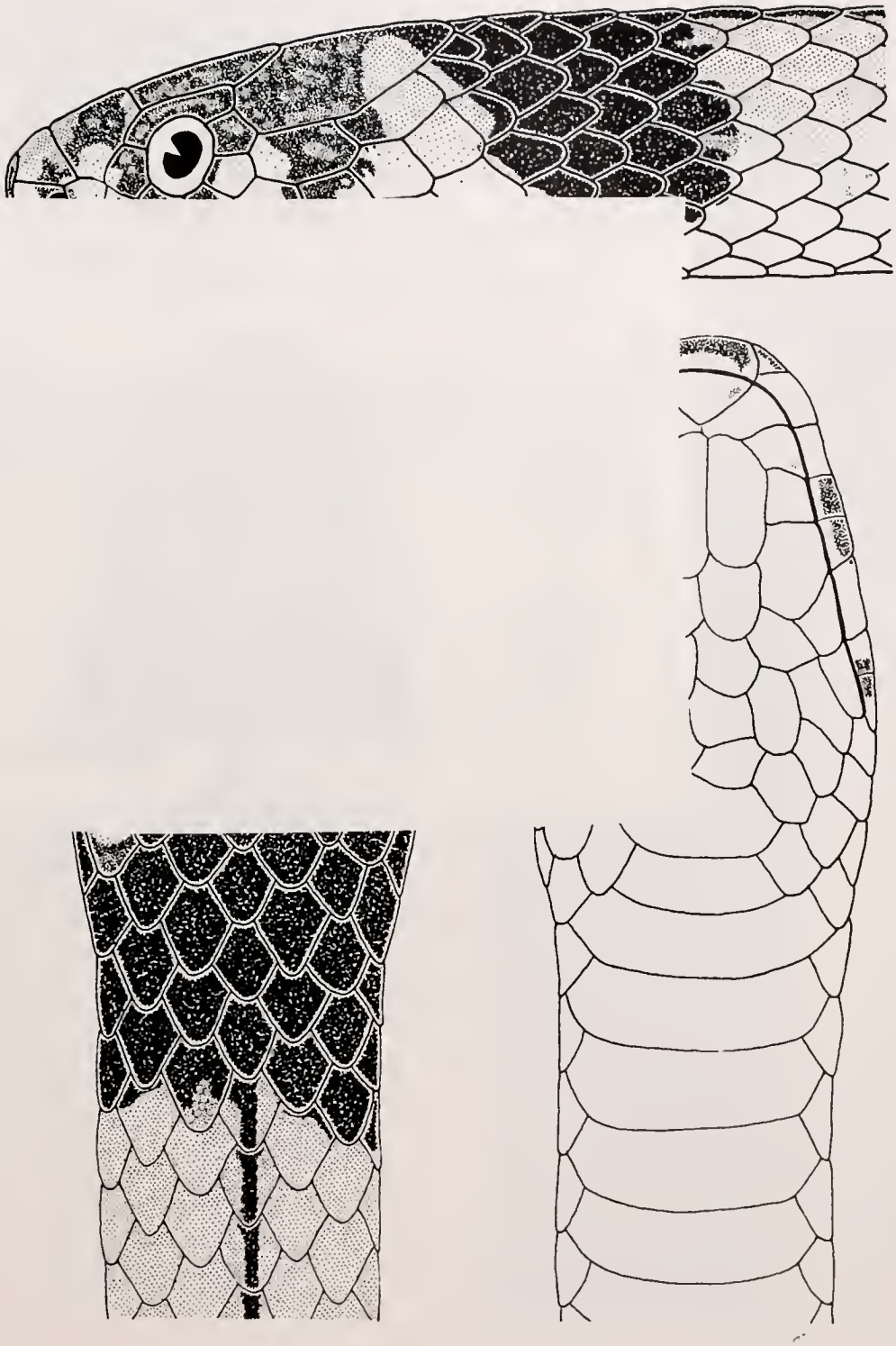
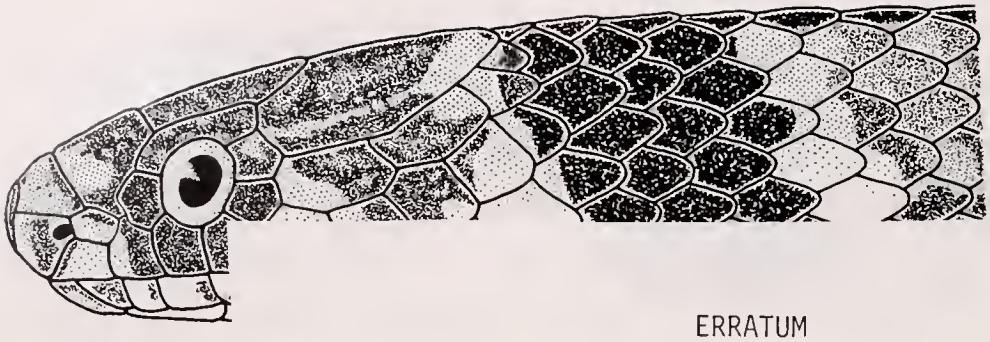


Fig. 4. Lateral, dorsal, and ventral views of head of a member of the pattern E group of *Tantilla melanocephala* (TCWC 38209, Centro Unión, Depto. Loreto, Perú).



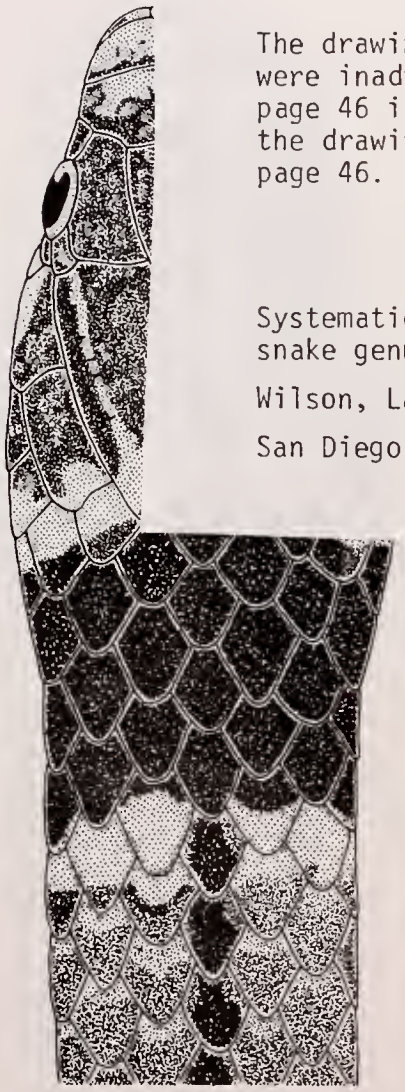
ERRATUM

The drawings, but not the captions, of Figs. 3 and 4 were inadvertently exchanged. That is, the drawing on page 46 is explained by the caption on page 47, and the drawing on page 47 is explained by the caption on page 46.

Systematics of the melanocephala group of the colubrid snake genus Tantilla.

Wilson, Larry David, and Cesar E. Mena.

San Diego Society of Natural History Memoir 11. 1980.



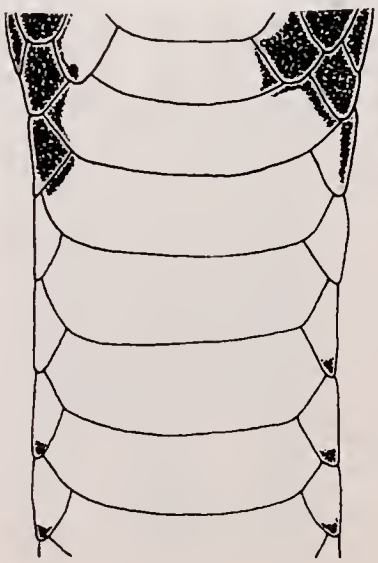


Fig. 3. Lateral, dorsal, and ventral views of head of a member of the pattern D group of *Tantilla melanocephala* (MBUCV III-1825, Guri, Est. Bolívar, Venezuela).

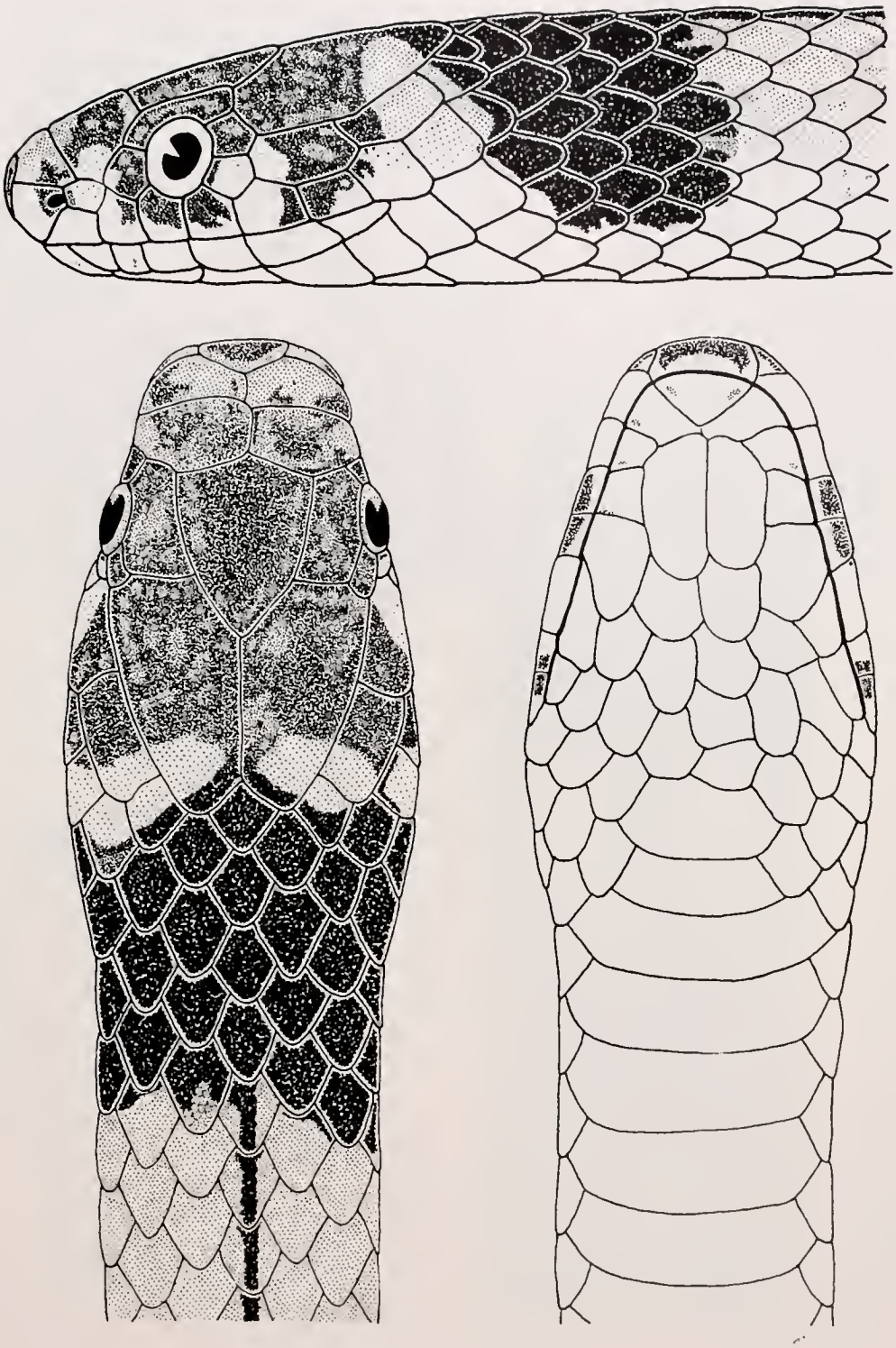


Fig. 4. Lateral, dorsal, and ventral views of head of a member of the pattern E group of *Tantilla melanocephala* (TCWC 38209, Centro Unión, Depto. Loreto, Perú).

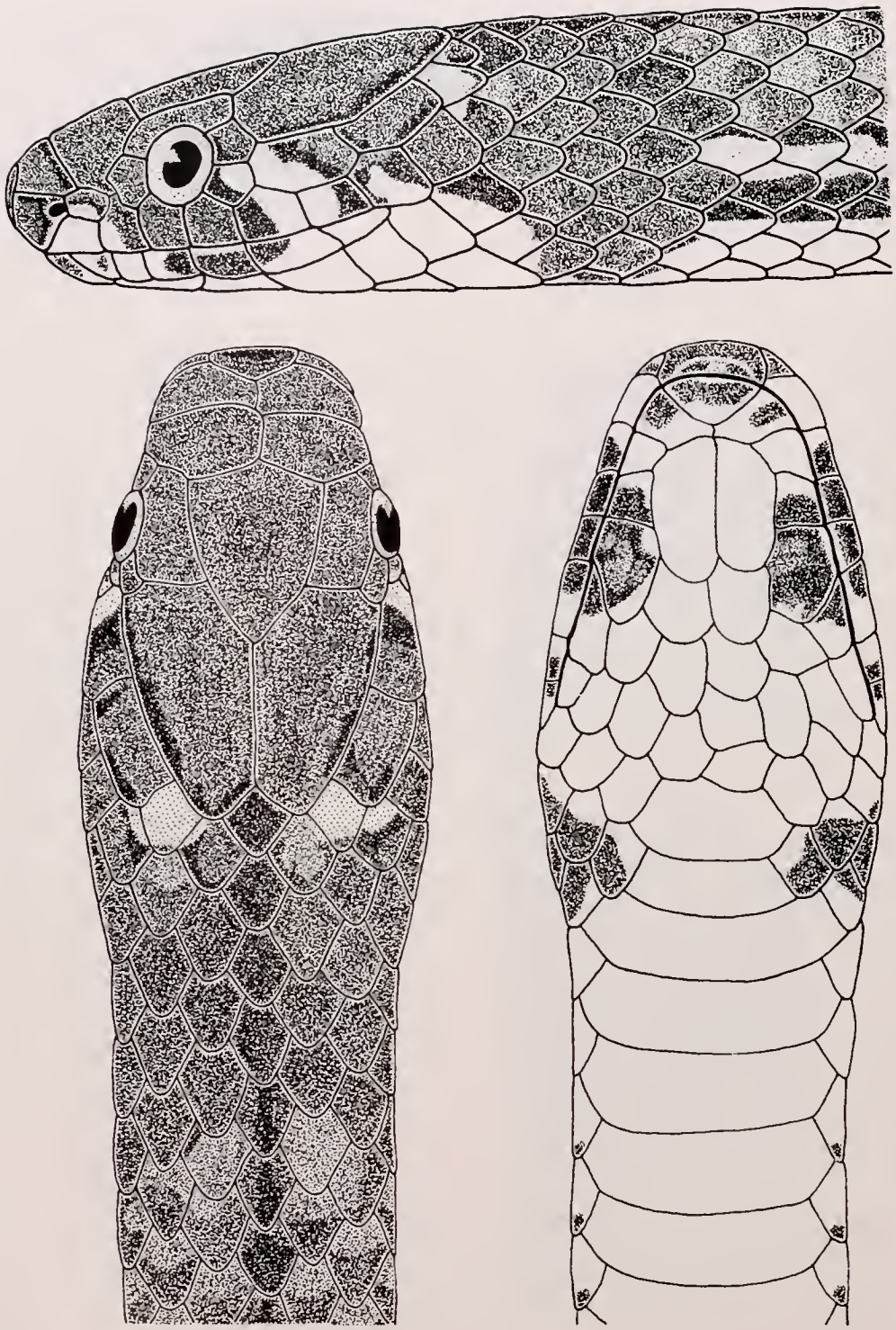


Fig. 5. Lateral, dorsal, and ventral views of head of a member of the pattern F group of *Tantilla melanocephala* (NMW 20366:1, Santo Domingo de los Colorados, Prov. Pichincha, Ecuador).

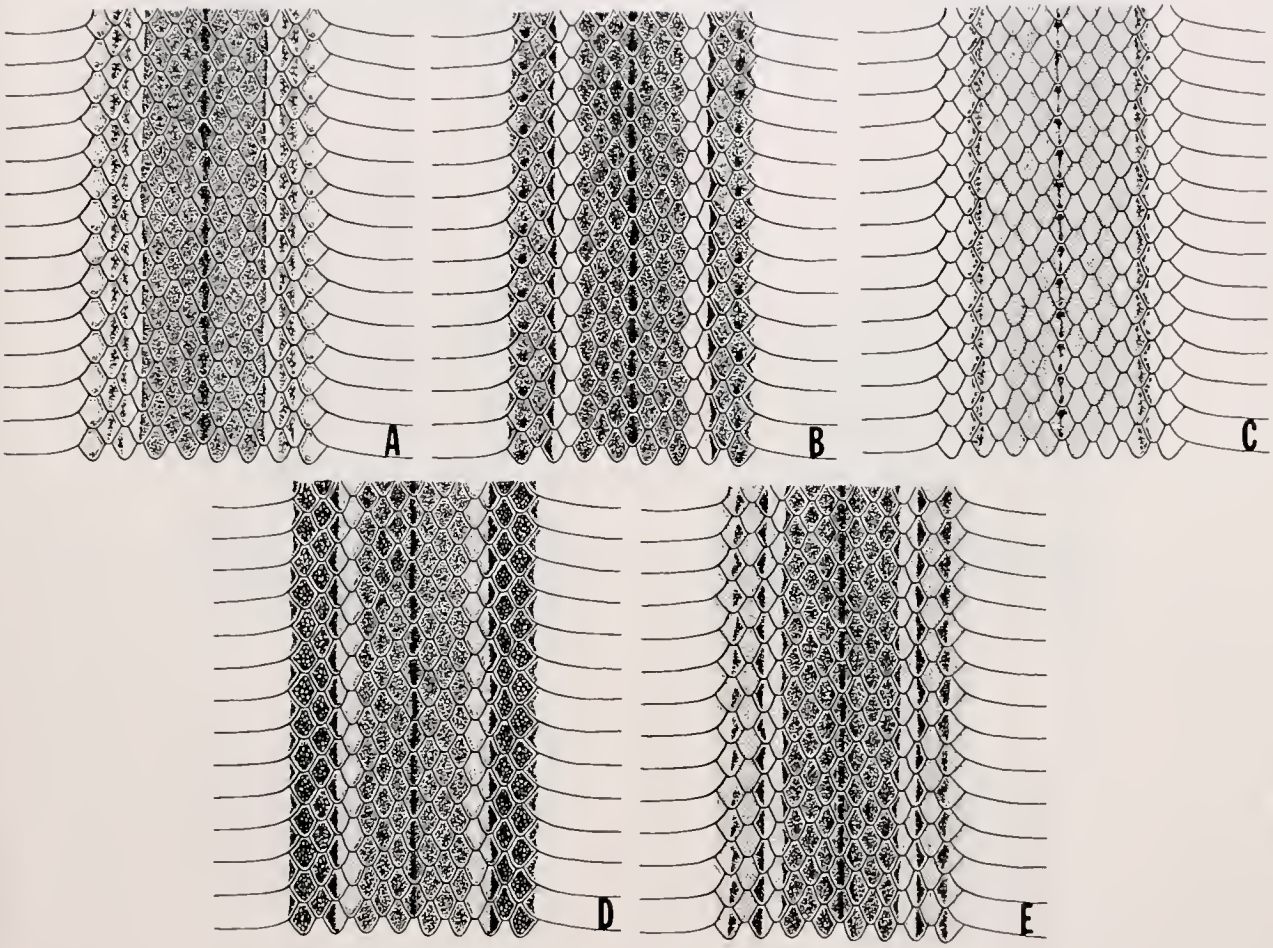


Fig. 6. Dorsal color patterns of members of five pattern groups of *Tantilla melanocephala:* (A) pattern A (KU 102529); (B) pattern B (KU 31960); (C) pattern D (MBUCV III-1825); (D) pattern E (TCWC 38209); (E) pattern F (NMW 20366:1). All locality data same as that for head figures.

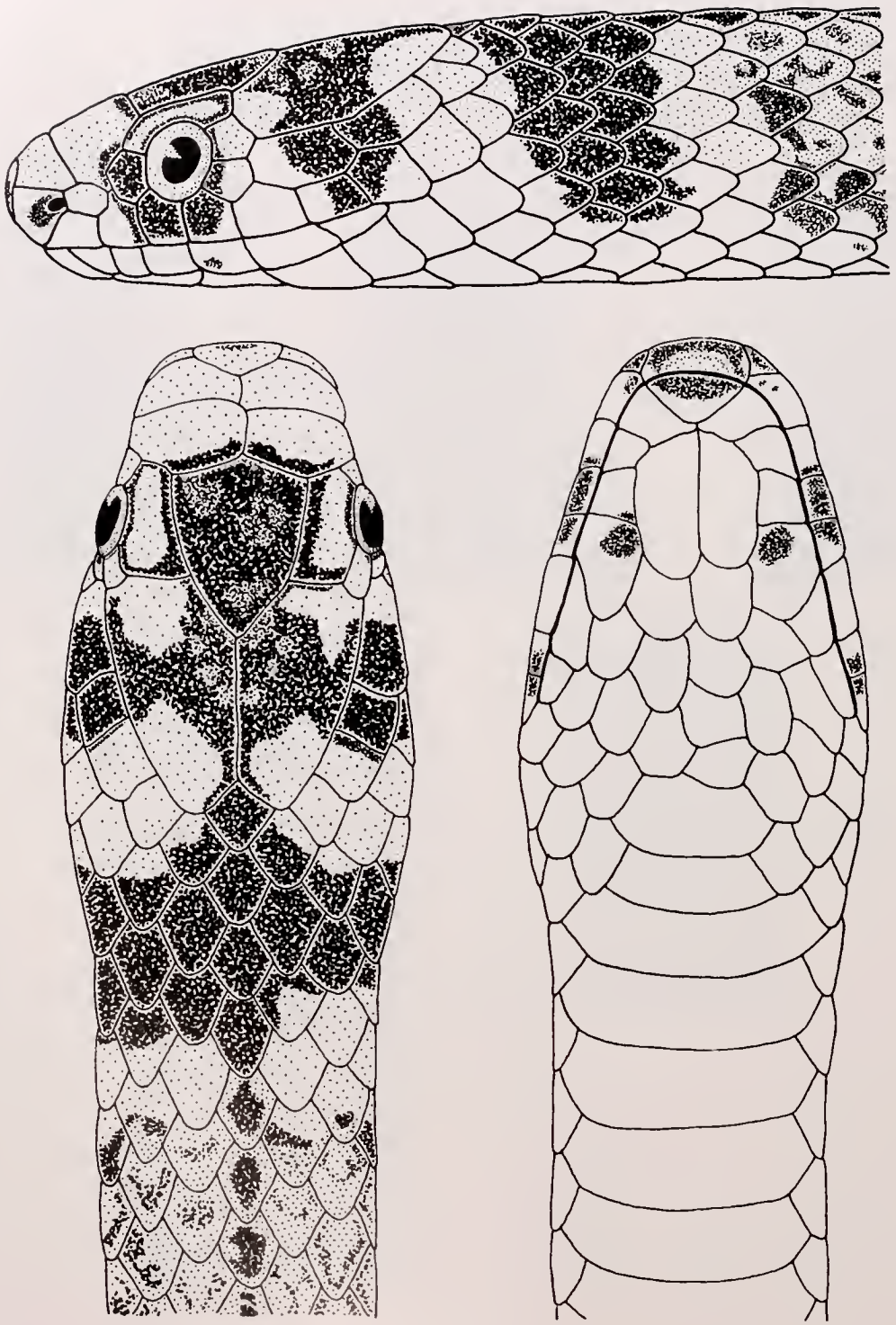


Fig. 7. Lateral, dorsal, and ventral views of head of *Tantilla andinista* (KU 135209, 5 km E Alausí, Prov. Chimborazo, Ecuador).

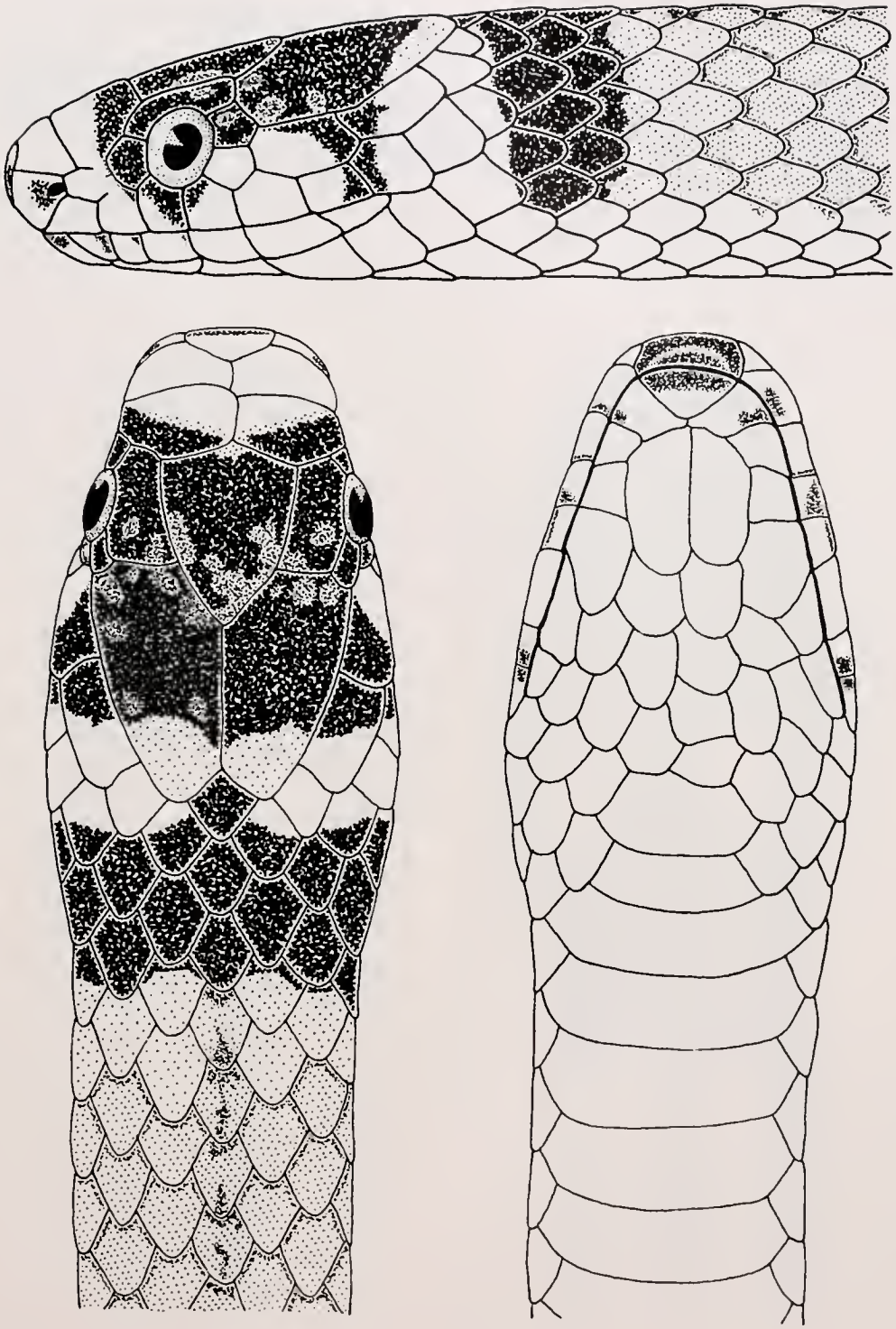


Fig. 8. Lateral, dorsal, and ventral views of head of *Tantilla capistrata* (FMNH 34287, Chiclin, Depto. La Libertad, Perú).

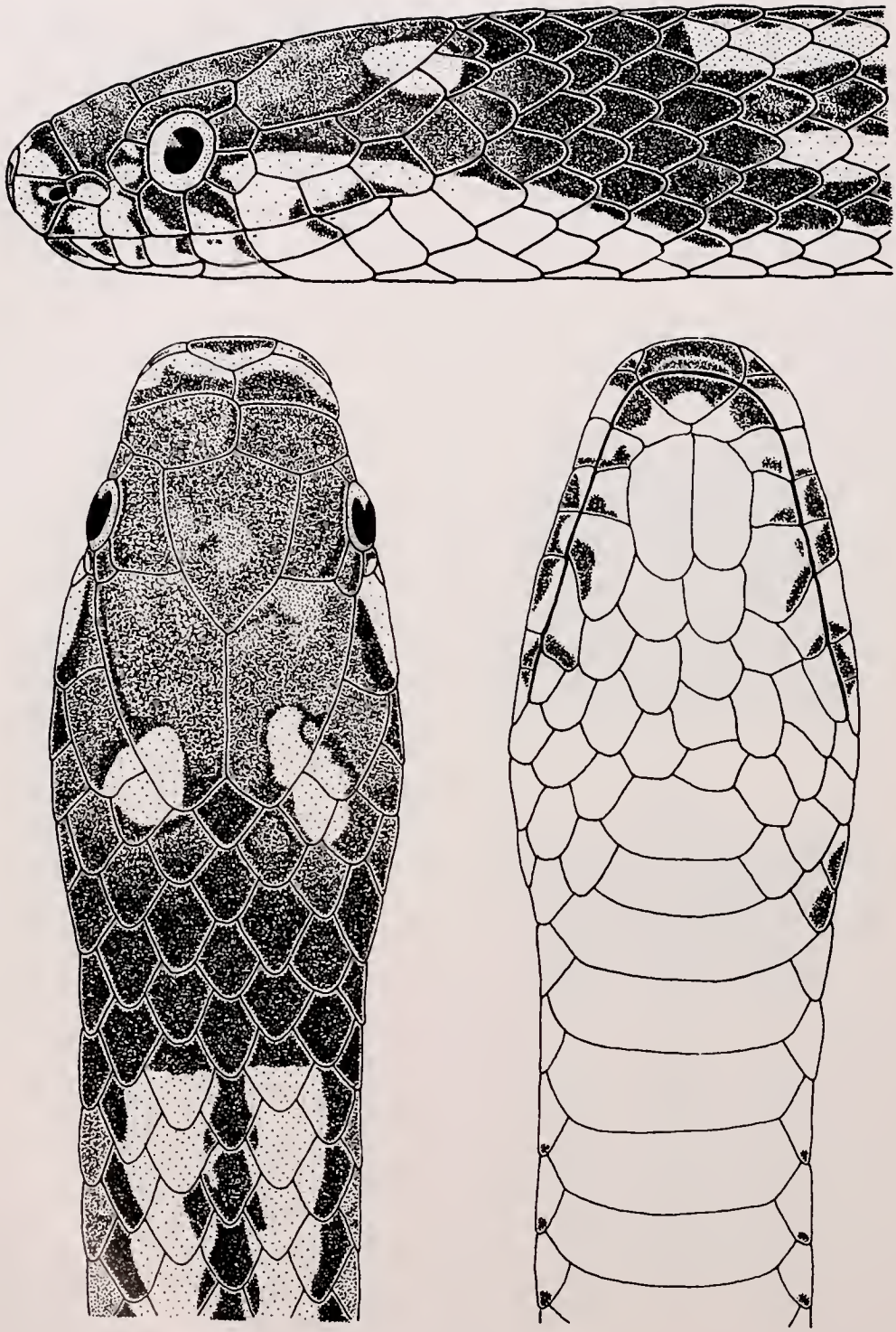


Fig. 9. Lateral, dorsal, and ventral views of head of *Tantilla equatoriana* (USNM 198530, San Lorenzo, Prov. Esmeraldas, Ecuador).

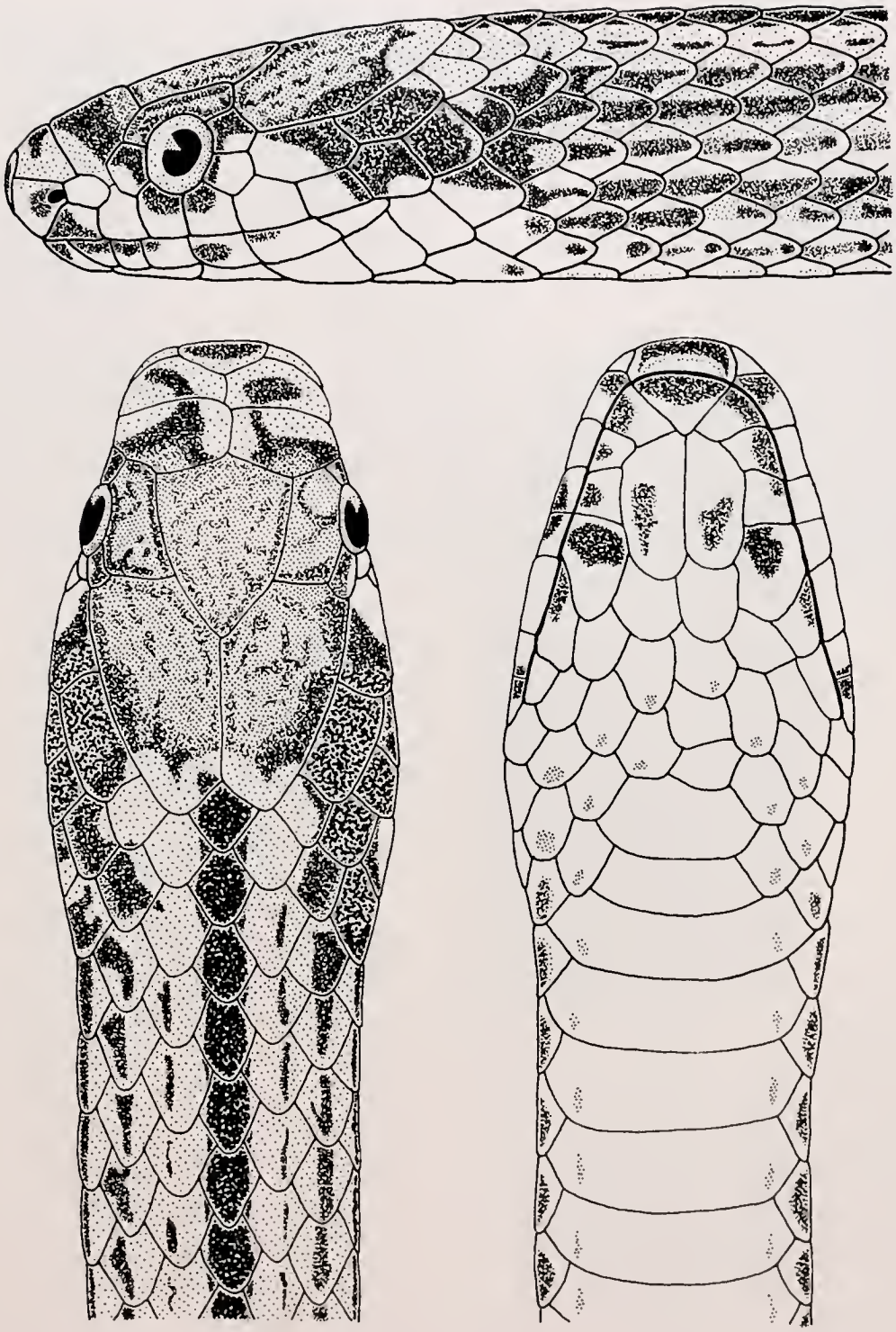


Fig. 10. Lateral, dorsal, and ventral views of head of *Tantilla insulamontana* (KU 152207, Río Minas, 15.1 km W Santa Isabel, Prov. Azuay, Ecuador).

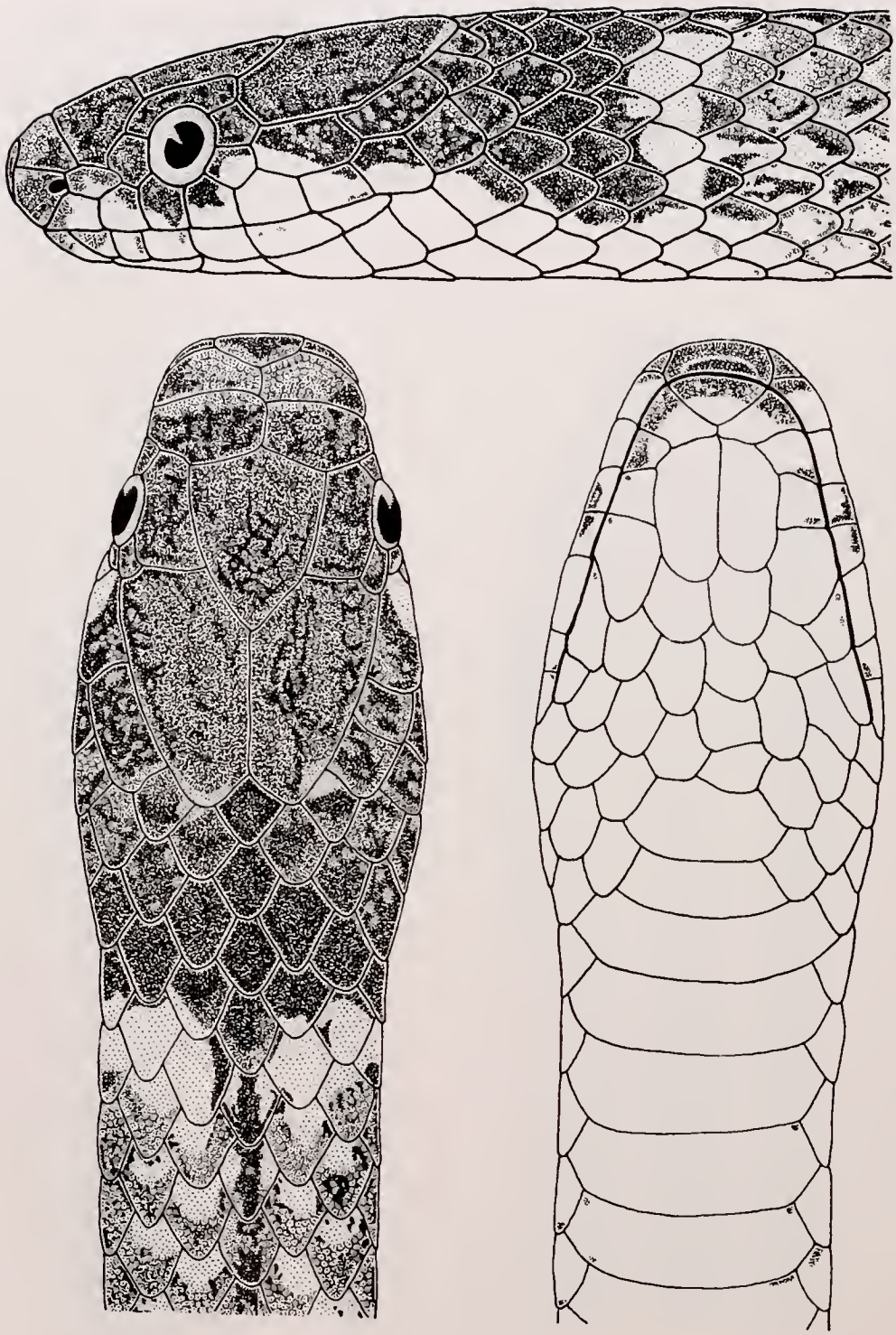


Fig. 11. Lateral, dorsal, and ventral views of head of *Tantilla lempira* (LSUMZ 26093, 41 km NW Tegucigalpa, Depto. Francisco Morazán, Honduras).

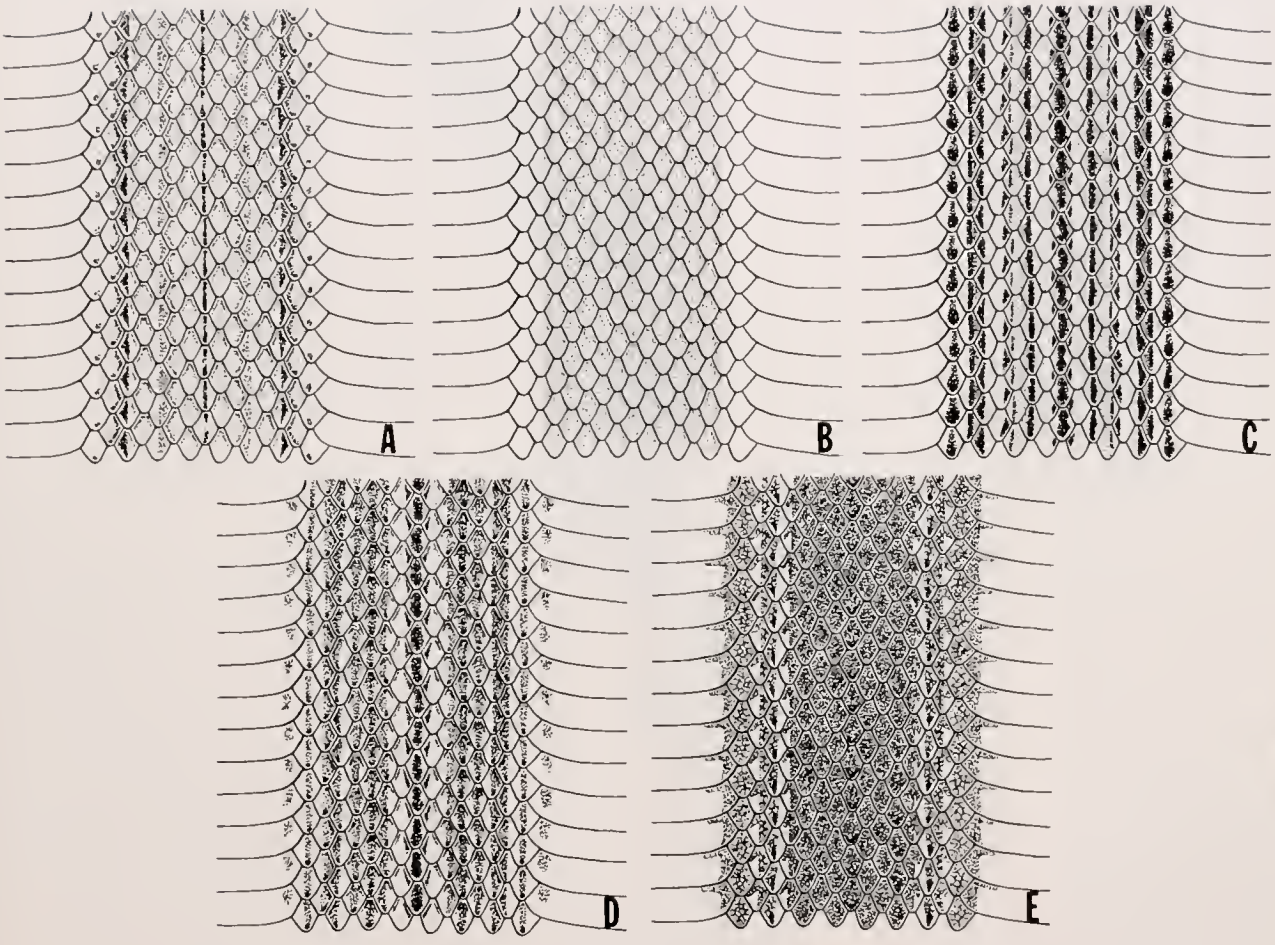


Fig. 12. Dorsal color patterns of 5 members of the *Tantilla melanocephala* group: (A) *T. andinista* (KU 135209); (B) *T. capistrata* (FMNH 34287); (C) *T. equatoriana* (USNM 198530); (D) *T. insulamontana* (KU 152207); (E) *T. lempira* (LSUMZ 26093). All locality data same as that for head figures.

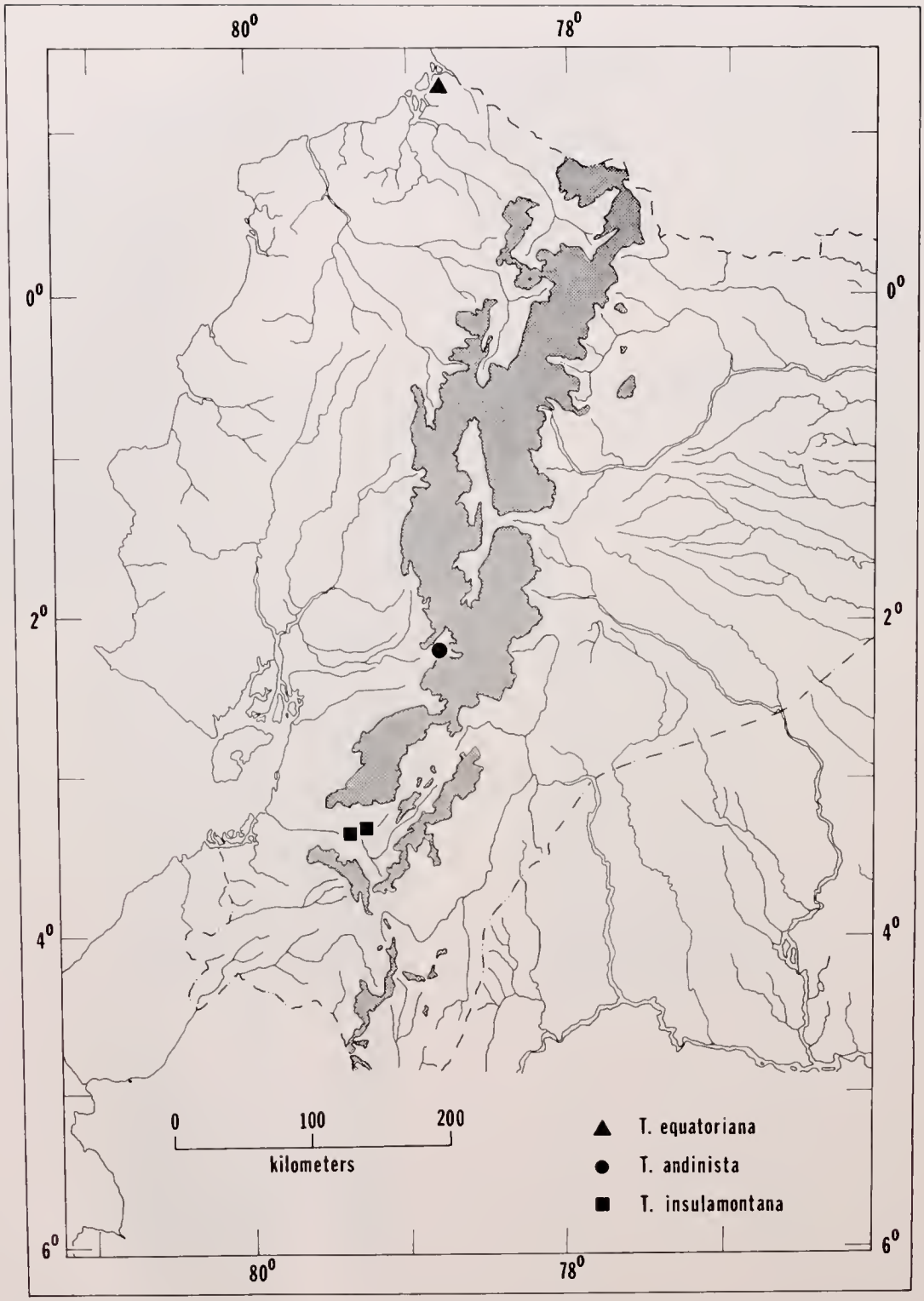


Fig. 13. Distribution of 3 members of the *Tantilla melanocephala* group.

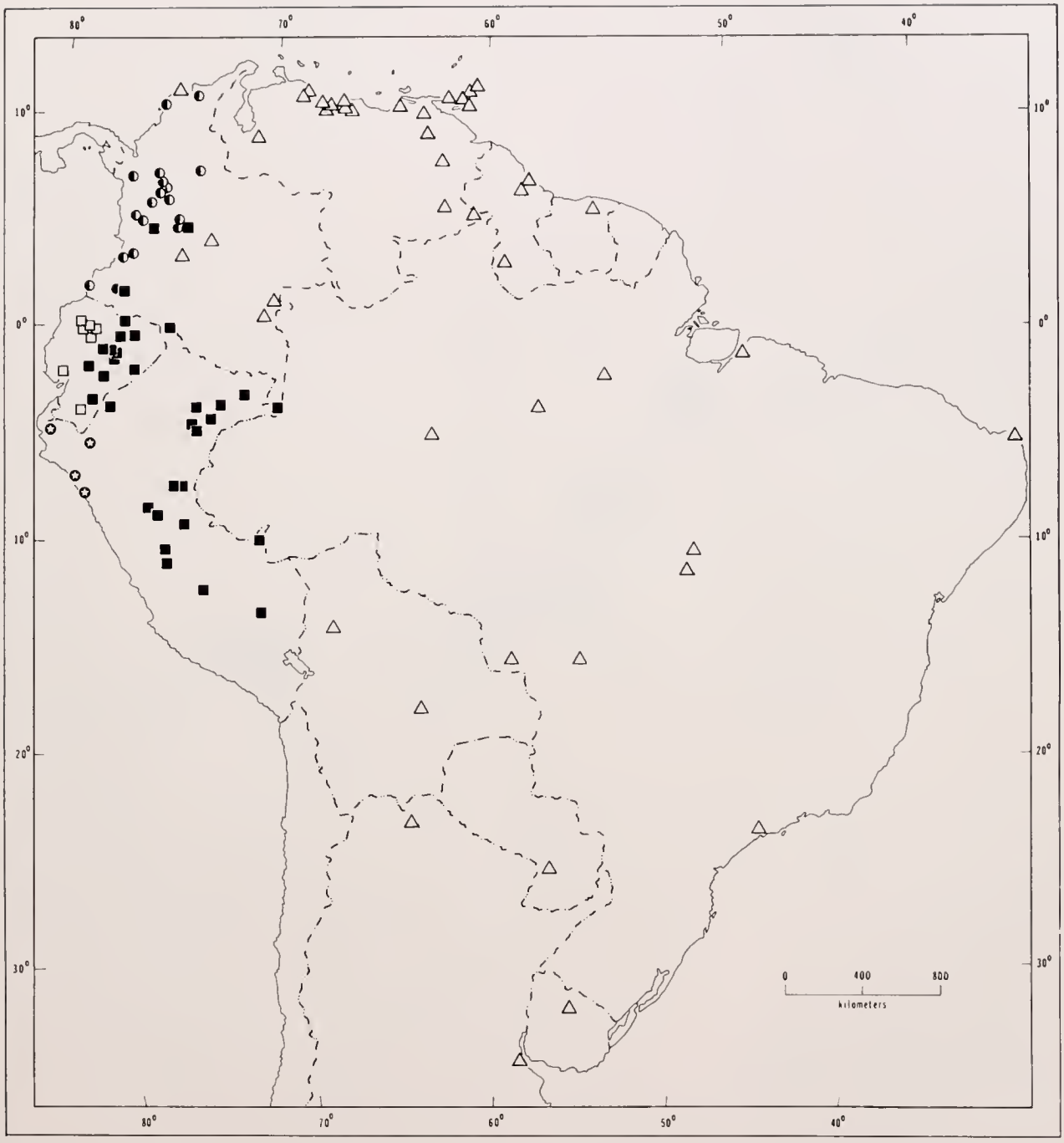


Fig. 14. Distribution of 4 pattern groups of *Tantilla melanocephala* (patterns C and D—triangles; pattern E—black squares; pattern F—open squares), *T. melanocephala* intermediates (half-open circles), and *T. capistrata* (circles with stars).

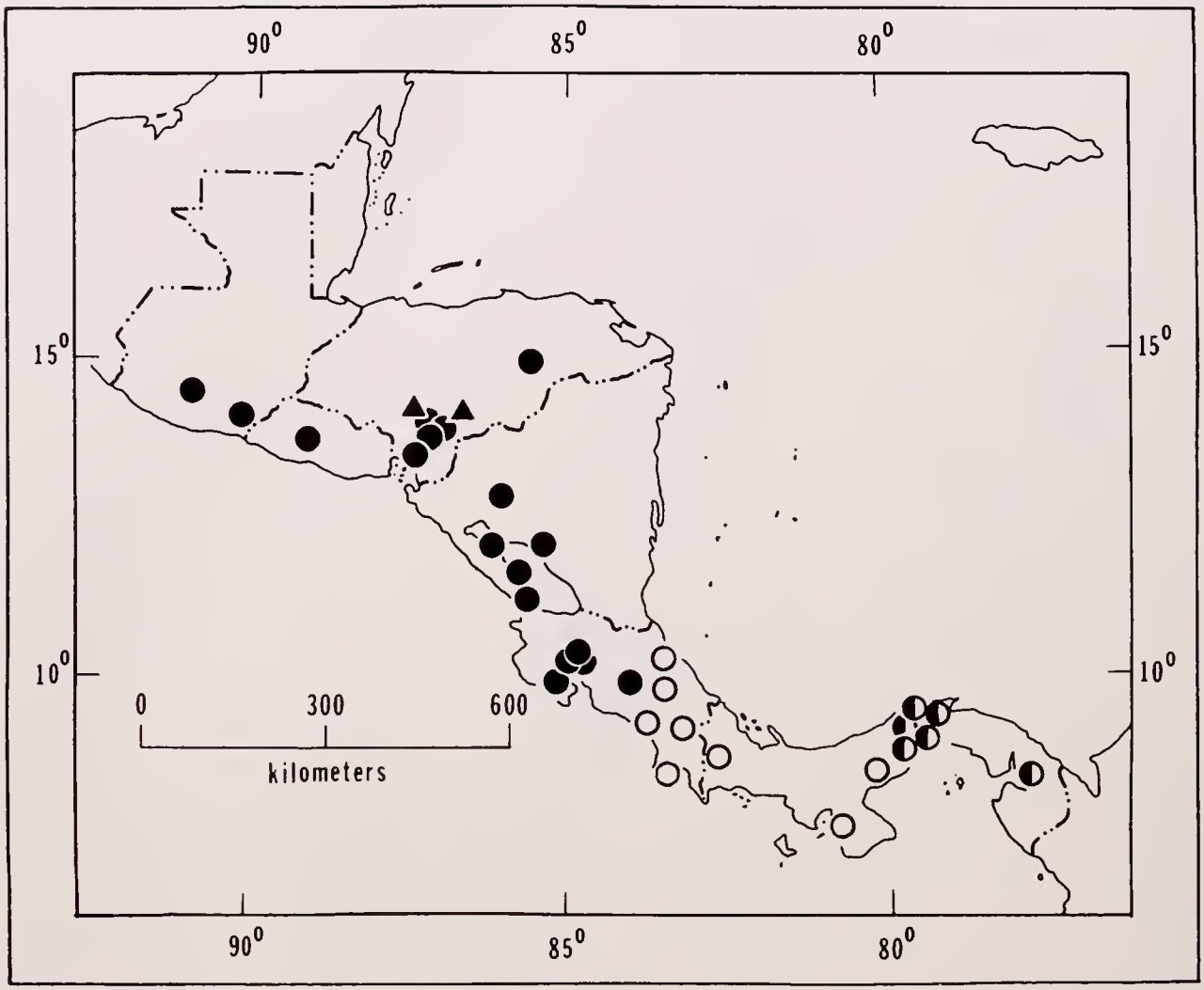


Fig. 15. Distribution of 2 pattern groups of *Tantilla melanocephala* (pattern A—black circles; pattern B—open circles), *T. melanocephala* intermediates (half-open circles), and *T. lempira* (triangles).

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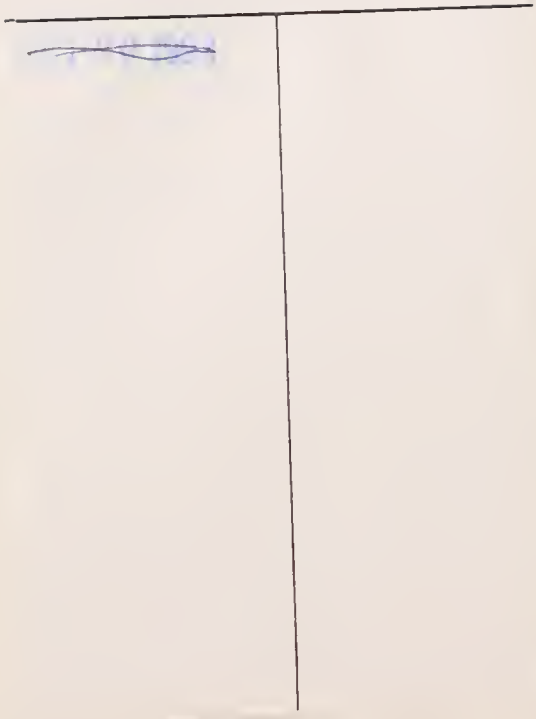

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